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ENHANCING SEEDLING EMERGENCE AND PRODUCTIVITY OF FORAGE GRASSES THROUGH THE MODELING OF SEED DORMANCY CHANGE

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Enhancing Seedling Emergence and Productivity of Forage Grasses Through Modeling of Seed Dormancy Changes

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Table of Contents

Table of Contents----------i

Abstract----------1

Executive Summary----------2

Acknowledgments----------3

Introduction----------4

Project Objectives----------5

Materials and Methods----------7

Part I: Effects of Temperature on Dormancy Change, Germination and the Application Of Thermal Time Models----------7

Part II: Seedling Emergence in the Field and its Prediction Using the Thermal Time Model-----12

Results----------15

Part I: Effects of Temperature on Dormancy Change, Germination and the Application Of Thermal Time Models----------15

Part II: Seedling Emergence in the Field and its Prediction Using the Thermal Time Model-----26

Discussion and Management Implications----------42

Literature Cited----------44

Abstract

The two western wheatgrass varieties (cv. Walsh and LC9078a) had deeper dormancy than the two orchardgrass varieties (cv. Artic and Lineta) Dormancy of both species was broken by temperatures with a 5-10C amplitude; this temperature variation is similar to that which occurs in the soil at a 1cm seeding depth. Optimal temperatures for germination of orchardgrass were broader than the optimal temperatures for germination of western wheatgrass. Seedling emergence of orchardgrass was less sensitive to seeding dates in the spring than western wheatgrass; seedling emergence of western wheatgrass increased as seeding dates were delayed from early May to late May when soil water was not limited. The rate of seedling emergence increased with increasing temperatures in both species, therefore; faster and more uniform seedling emergence can be expected from late seeding dates.

Seedling emergence of orchardgrass in the field is usually less then the germination percentage obtained in the laboratory because light exposure during germination tests can break dormancy in orchardgrass seeds and the small seeds or orchardgrass have limited energy reserves for pre-emergence seedling growth. On the other hand, germination of western wheatgrass seeds can be reduced by exposure to light during germination and seeds are larger than those of orchardgrass. Therefore, seedling emergence of western wheatgrass in the field is usually greater than germination test would predict. The use of thermal time models to study seed dormancy changes and germination revealed the dual effects of temperature for threes processes. The modified thermal time model takes the difference between germination and seedling emergence into account and it can accurately predict (R^2= 0.92 to 0.99) seedling emergence in the field.

Executive Summary

Forage crops are a source of major feed and nutrients for domestic and wild animals. Forages also play important roles in soil conservation and improvement. Uniform seedling emergence is important for establishment and production of forages. However, dormancy in seeds of forages prevents the accurate determination of seeding rates because field conditions affect dormancy changes and seedling emergence. The main objective of this project was to quantify dormancy changes in two varieties (cv. 'Arctic' and Lineata') of orchardgrass (*Dactylis glomerata* L.) and two varieties (cv. 'Walsh' and 'LC9078a') of western wheatgrass (*Pascopyrum smithii* (Rydb.) L.) under field conditions. Field experiments were conducted near Saskatoon, Saskatchewan in 2003 and 2004 with four seeding dates ranging from early May to mid-June. Seeds were also buried in the field and retrieved regularly to determine the fate of seeds as affected by field conditions. Laboratory experiments were also conducted to determine the effects of temperature on changes in seed dormancy.

The daily temperature at the 1 cm seeding depth in the field averaged between 5 and 20°C between the first and the last seeding dates and diurnal temperatures fluctuated about 10°C. Germination tests in the laboratory indicated that this temperature fluctuation was within the optimal range of temperatures for breaking of dormancy and germination of both species. A broad range of temperatures (e.g. 10-25°C) were optimal for germination of orchardgrass, but the optimal temperature for germinaiton of western wheatgrass germination was 15°C. These differecnes in optimal temperatures for germination explained the observed differences in seedling emergence between species and seeding dates in the field. Seedling date had little influence on the final seedling emergence of orchardgrass. By comparison, seedling emergence of western wheatgrass increased with seeding date until late May and decreased in early June; changes in seedling emergence corresponded with changes in soil temperatures. Seedlings emerged from late spring seeding dates in the Northern Great Plains, however, may have to face the adverse environmental conditions such as drought.

Seeds of both species were dormant with western wheatgrass having a deeper dormancy (< 20% germination at all constant temperatures) than orchardgrass (<50% at constant temperatures less than 15 or greater than 30°C). Alternating temperatures broke dormancy in both species. A 5°C temperature difference was sufficient to break dormancy in seeds of orchardgrass while western wheatgrass required a 10°C temperature amplitude to the break dormancy in seeds. A temperature amplitude greater than 10°C did not further enhance germination. Seed mortality within eight weeks of seeding was low (mostly <10%) in the field. Germination of both species was sensitive to brief exposure to light especially under unfavorable temperatures. Germination of orchardgrass was enhanced by exposure of seeds to light and while germination of western wheatgrass was inhibited by light. Seedling emergence from on the soil surface was generally greater than seed germination in Petri dishes for western wheatgrass, possibly due to the inhibiting effect of light on seeds in Petri dishes. Seedling emergence of orchardgrass, however, was usually less than seed germination in Petri dishes, possibly because of an enhancing effect of light on seed germination in Petri dishes and also because of seedling mortality in the soil..

A modified thermal time model accurately predicted seedling emergence in the field for both orchardgrass varieties (R^2 =0.92 to 0.99) when soil water was not limiting. The high correlation between germinaiton tests and seedling emergence in the field is attributed to the use of alternating temperature regimes for the construction of thermal time models and the

modification of thermal time models developed in the laboratory for seedling emergence. For western wheatgrass, however, thermal time models could not be constructed because the linear relationship between germination rate and temperature could not be established due to deep dormancy of seeds. This study quantified the effect of field conditions on seedling emergence of orchardgrass and western wheatgrass. Seeding rates for field seedings of orchardgrass can be accurately developed from laboratory germination and emergence tests, but the same cannot be done for western wheatgrass. An alternative way to construct the thermal time model for western wheatgrass is to first break seed dormancy using alternating temperature treatment, then establish the relationship between germination rate and constant temperatures. It is likely that thermal time models for predicting seedling emergence in the field can also be developed for most forages; however, variety and species specific parameters must be developed for the models.

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Introduction

Forage crops provide major food source of nutrients for domestic and wild animals along with playing important roles on soil conservation and improvement. There are about 30,000 forage growers and more than 2.8 million acres land for hay production in Saskatchewan (Saskatchewan Agriculture, Food and Rural Revitalization, 2005). The value of the hay produced is approximately $260 million annually. More land base may become available for hay production as the result of the Green Cover Program (Saskatchewan Agriculture, Food and Rural Revitalization, 2004). The potential for increasing forage production on these lands exist and management practices that can enhance uniform seedling emergence and stand establishment may help reach these potential.

Seedling emergence in the field is the combined result of seed germination after dormancy release and pre-emergence seedling growth in the field (Vleeshouwers, 1997). Therefore, it is not surprising to observe disagreement between seedling emergence in the field and germination tests in the laboratory. Soil temperature is the most important factor affecting seedling emergence when water is not limiting (Vleeshouwers and Kropff, 2000). The response of seed germination rate to temperature after dormancy release is linear below and above an optimum value (Garcia-Huidobro et al., 1982a, b; Bauer et al., 1998). Thermal time models have been used to predict seed germination and seedling emergence in relation to soil temperatures (Covel et al., 1986; Del Monte and Tarquis, 1997; Moot et al., 2000). However, most forage species have different degrees of seed dormancy, which in turn restricts the application of thermal time models on these species.

Temperatures in the field regulate seed germination in two ways: 1) breaking dormancy by fluctuating temperatures (Benech-Arnold et al., 1988); and 2) determining the germination rate of seeds after dormancy has been released (Garcia-Huidobro et al., 1982a). The dual functions of temperature in seed dormancy and germination make the quantitative prediction of dormancy change and seedling emergence difficult. Thermal time models are usually developed by using reduction steps to separate dormancy change and seed germination based on germination tests at constant temperatures after dormancy breaking treatments, which does not accurately reflect the processes in the field because of the dual roles of temperature occur simultaneously. Thus, the dual roles of the temperature must be considered for seeds with dormancy in the construction of thermal time model for the prediction of seedling emergence in the field. Nevertheless, due to the complexity of seedling emergence as affected by pre-germination and post germination events in the field modifications of germination based thermal time models are necessary.

Orchardgrass (*Dactylis glomerata* L.) and western wheatgrass (*Pascopyrum smithii* (Rydb.) L.) are two common forage species in Saskatchewan. Seed dormancy of both species can be released by alternating temperatures (Toole, 1976; Pannangpetch and Bean, 1983). Using germination percentage to determine seeding rate is not reliable for these species and seedling emergence in the field was often lower for orchardgrass but higher for western wheatgrass than the germination percentage tested prior to seeding (B. Coulman and J.T. Romo, personal observations). The interaction of environmental factors, other than temperature, such as light and germination medium, may also be responsible for the disparity between seed germination in the laboratory and seedling emergence in the field. We hypothesized that 1) the dual roles of temperature on dormancy and germination can be described by thermal time model; and 2) thermal time model can be used to predict seedling emergence in the field after modification.

Project Objectives

The objectives of this research were to: 1) quantify the effect of alternating temperature on dormancy breaking in two varities of orchardgrass and western wheatgrass; 2) construct thermal time models for the dormancy change and germination as affected by temperature; 3) determine the seedling emergence as affected by temperatures in the field, and; 4) predict dormancy change and seedling emergence in the field using a modified thermal time model.Materials and Methods

Part I: Effects of Temperature on Dormancy Change, Germination and the Application Of Thermal Time Model

1. Seed sources

Two species, orchardgrass and western wheatgrass, were used in this experiment. Two varieties for each species, 'Arctic' and 'Lineta' for orchardgrass, and 'Walsh' and 'LC9078a' for western wheatgrass, were chosen. Seeds were cleaned using a seed blower by controlling airflow at a fixed speed for 1.5 minutes. Seeds blown up to the upper container of the blower were discarded and the sediments were saved. Cleaned seeds were stored at –18°C until use. A 0.05% benomyl powder was applied to seed surface for sterilization at the beginning of germination tests.

2. Seed germination tests for model construction

Germination tests were conducted at 28 constant and alternating temperature regimes in growth chambers (Sanyo Versatile Environment Chamber MLR-350H, Sanyo Scientific, USA). Constant temperatures with 5°C increment between 0 and 35°C and alternating temperatures with amplitudes from 5 to 20°C were used (Table 1). A randomized complete block design (RCBD) with five replicates was used and replicates were put into growth chambers at weekly intervals. Designated temperatures were randomly allocated to each growth chamber. For each replicate, a unit of 50 seeds was imbibed on top of two layers of filter paper (Whatman No.1) in 9 cm plastic Petri dishes. The filter paper was moistened with 5 ml distilled water and seeds were then carefully spread on top of the paper. Twenty Petri dishes (four varieties x five replicates) were randomized within each chamber in darkness. Clear plastic bags were used to seal Petri dishes to reduce water evaporation. Seeds were sprayed with 0.05% benomyl solution whenever there was a sign of microorganism contamination during germination tests.

Temperatures inside the growth chambers were monitored continuously using dataloggers (21X, Campbell Scientific Inc., USA) and recorded at hourly intervals using two or three probes per chamber which were randomly placed in three middle shelves. Recorded temperatures were used in thermal time modeling.

Table 1. Treatment design of constant and alternating temperatures with temperature amplitude from 0 to 20°C and a 5°C increment.

	Temperature amplitude (°C)				
Mean temperature (°C)	0	5	10	15	20
0	0/0				
5	5/5	2.5/7.5	0/10		
10	10/10	7.5/12.5	5/15	2.5/17.5	0/20

15	15/15	12.5/17.5	10/20	7.5/22.5	5/25
20	20/20	17.5/22.5	15/25	12.5/27.5	10/30
25	25/25	22.5/27.5	20/30	17.5/32.5	15/35
30	30/30	27.5/32.5	25/35		
35	35/35				

Germinated seeds were counted and removed at 24-hour intervals;seeds with shoot greater than 3 mm were considered germinated. Distilled water was added when necessary to keep the germination blotters wet. Germination tests were terminated when no seeds germinated for 14 consecutive days. Petri dishes containing seeds were then transferred to 15/25°C for continuous germination, which was the optimal temperature for the germination of the two species based on preliminary tests. Seed germination was also recorded at 24-hour intervals. If no seeds germinated for 14 consecutive days, the number of viable seeds (seeds with firm embryos by pressing) and dead seeds were recorded. The highest mean seed viability among all the temperature regimes of each variety was chosen as the viability for the variety (Wang et al., 2004).

3. Estimating germination rates for different sub-populations using Chapman-Richards growth function

A germination time course curve was constructed for each germination temperature regime and each variety using Chapman-Richards growth function (Richards, 1959; Lee, 2002). The Chapman-Richards growth function can take the following form:

$$g = m(1-\exp(-nt))^p \qquad \text{(Eq. 1)}$$

where g = germination percentage, t = time, m = the asymptote, n = the rate parameter, and p = the shape parameter. The three parameters, m, n, and p, are constants. A sigmoid growth form has an asymptote (parameter m) for the maximum germination percentage. The n and p parameters together define the shape of the curve.

For modeling purposes, a seed population is considered to be composed of sub-populations based on relative germination rate (Garcia-Huidobro et al., 1982b). A nonlinear regression procedure with the Levenberg-Marquardt algorithm method (PROC NLIN, SAS, 1995; Marquardt, 1963) was used to estimate parameters (a, b, and c) for the Chapman-Richards growth function and germination time (t_g) for the 10, 20, 30, 40, 50, 60, 70, 80, and 90% sub-populations wherever available. Multiple starting values for parameters were provided to ensure that the nonlinear least square solution was a global minimum rather than a local minimum (Schabenberger and Pierce, 2002). The germination time for each subpopulation was calculated based on the Chapman-Richards function and used to calculate germination rate for the construction of thermal time model. Since there is no real coefficient of determination (R^2) for nonlinear models, model fit was measured using Pseudo-R^2 as follows (SAS, 1995):

$$\text{Pseudo-}R^2 = 1 - \text{SS(Residual)}/\text{SS(Total}_{\text{Corrected}}\text{)} \qquad \text{(Eq. 2)}$$

where Pseudo-R^2 = approximately value used to measure model fit, SS(Residual) = sum of squares of the residual, and SS(Total$_{\text{Corrected}}$) = sum of squares of the corrected total.

4. Estimating and testing base temperature and thermal time

Germination rate for different sub-population g ($GR_{(g)}$) was calculated with the reciprocal of germination time ($1/t_g$). Base temperature (T_b) and thermal time of orchardgrass and western wheatgrass at both constant and alternating temperatures was estimated using extrapolation (graphical) methods (Garcia-Huidobro et al., 1982a). Unlike the conventional method using $GR_{(g)}$ as the dependent variable and plotted on temperature (Garcia-Huidobro et al., 1982a, b; Kebreab and Murdoch, 1999; Steinmaus et al., 2000), temperature was treated as the dependent variable and plotted on $GR_{(g)}$. The intercept of the linear regression line was T_b and the linear relationship between temperature T and $GR_{(g)}$ varies among sub-populations in the slope of the regression line, which equals to the thermal time ($\theta_{(g)}$) (Eq. 3).

$$T = T_b + \theta_{(g)} GR_{(g)} = T_b + \theta_{(g)} \frac{1}{t_{(g)}} \qquad \text{(Eq. 3)}$$

In order to estimate the common T_b, linear regression model of T on $GR_{(g)}$ for the available sub-populations with successive increment of 10% were established. Nonlinear regression models composed of all the linear regression functions were then constructed within the same temperature amplitude for each variety. Actual recorded temperatures of growth chambers were averaged over the time required for germination of sub-populations and used for thermal time modeling. The range of sub-optimal temperatures as determined based on visual inspection of the linearity of $GR_{(g)}$ over temperature (Wang et al., 2004) and subpopulations containing at least three temperature points were used to estimated T_b and $\theta_{(g)}$. A sum of square reduction test (Schabenberger and Pierce, 2002) was used to assess whether there was a common T_b among the available subpopulations. The full model was composed of different T_b's and $\theta_{(g)}$'s for the available subpopulations. The reduced model was composed of one common T_b and different slopes for the subpopulations. The following equation was used for the sum of square reduction test:

$$F = \{(SS_{(Residual)}Reduced - SS_{(Residual)}Full)/(df_{(Residual)}Reduced-$$

$$df_{(Residual)}Full)\}/MSError_{(Full)} \qquad \text{(Eq. 4)}$$

If the result of this test showed that the full and the reduced models were not significantly different, a common T_b was used for all subpopulations and the slopes of subpopulations based on the common T_b were $\theta_{(g)}$'s.

5. Estimating nonlinear thermal time model parameters

Base temperature and thermal time were estimated for different temperature amplitudes in the previous section for each variety. Subsequently, thermal time models were constructed for each temperature amplitude and variety by using the Champman-Richards growth function. The model took the following form:

$$g = a(1 - \exp(-b\theta_{(g)}))^c \qquad \text{(Eq. 5)}$$

where g = germination percentage, $\theta_{(g)}$ = thermal time for sub-population g, a = the asymptote, b = the rate parameter, and c = the shape parameter. The three parameters, a, b, and c, are constant.

According to Equation (3), the cumulative thermal time for the actual observed seed germination under fluctuating temperature regimes can be described as:

$$\theta_{(g)} = \sum_{i=1}^{t}(T_i - T_b) = (\bar{T} - T_b)t \qquad \text{(Eq. 6)}$$

Combining Eq. 5 and Eq. 6 resulted in the nonlinear thermal time model for germination:

$$g = a(1 - \exp(-b(\sum_{i=1}^{t}(T_i - T_b))))^c = a(1 - \exp(-b(\bar{T} - T_b)t))^c \qquad \text{(Eq. 7)}$$

where g = germination percentage, a = the asymptote, b =the rate parameter, c = the shape parameter, t=time, T_i = temperature at time i, $\bar{T}$ =mean temperature for time i, T_b = base temperature, and $\theta_{(g)}$ = thermal time for the g subpopulation to germinate.

The biological meaning of the parameters can be reflected from the first and second derivatives of Eq. 7. The first derivative of the function Eq. 7 has the following expression:

$$\frac{\partial g}{\partial t} = ca(1 - \exp(-b(\bar{T} - T_b)t))^{c-1} \cdot b(\bar{T} - T_b)\exp(-b(\bar{T} - T_b)t) \qquad \text{(Eq. 8)}$$

Eq. 8 can be used to describe daily germination. The highest value of $\partial g / \partial t$ is the inflection point at which the daily germination reaches the highest at a certain time. The second derivative identifies the point where the germination rate changes:

$$\begin{aligned}\frac{\partial^2 g}{\partial t^2} = &\left[ca(1-\exp(-b(\bar{T}-T_b)t))^{c-1} \cdot -(b(\bar{T}-T_b))^2 \exp(-b(\bar{T}-T_b)t)\right] \\ &+\left[\begin{matrix} b(\bar{T}-T_b)\exp(-b(\bar{T}-T_b)t)\cdot(c-1)(ca)(1-\exp(-b(\bar{T}-T_b)t))^{c-2} \\ \cdot(-b)(\bar{T}-T_b)\exp(-b(\bar{T}-T_b)t)\end{matrix}\right]\end{aligned} \qquad \text{(Eq. 9)}$$

6. Model validation

Model validation were based on the coefficient of determination (R^2) of the linear regression analysis of predicted versus observed germination percentage, root mean square error (RMSE), sum of the residuals (SRES), and sum of the absolute residuals (SARES):

$$RMSE = \left[\frac{\sum_{i=1}^{n}(OBS_i - PRED_i)^2}{n}\right]^{\frac{1}{2}} \qquad \text{(Eq. 10)}$$

$$SRES = \sum_{i=1}^{n}(OBS_i - PRED_i) \qquad \text{(Eq. 11)}$$

$$SARES = \sum_{i=1}^{n} |OBS_i - PRED_i| \qquad \text{(Eq. 12)}$$

where OBS = % of observed seed germination, PRED = % of predicted seed germination. Germination percentage for 95% of the maximum observed data was used to validate the thermal time models.

A small RMSE suggests a close agreement between simulated and observed values. SRES is the relative measure of disagreement between observed and simulated germination percentage, and SARES is a measure of absolute precision of models (McMaster et al., 1992). The SRES and SARES are useful in determining how errors of each pair of data points in the model cancel. If SRES is small compared to SARES, errors in the model tend to cancel. If SRES and SARES are large and SRES is positive, the model tends to underestimate the germinate percentage (i.e. the simulated germination is lower than the observed germination). However, if SRES is negative and large as compared to SARES, the model tends to overestimate the germinate percentage (i.e. the simulated germination is higher than the observed germination) (McMaster et al., 1992).

7. Supplementary experiments

Several supplementary experiments were conducted to determine the effects of experimental conditions and seed treatments during germination tests on thermal time models. An experiment was designed to test possible the duration of light exposure during germination check on seed germination rate and total germination percentage. Four durations, 0, 5, 10 and 15 minutes of exposure and two temperature regimes, 15/25 and 5/15°C, were used. This was a randomized complete block design with five replicates and replicates were put into growth chambers at weekly intervals. For each replicate, a unit of 50 seeds was imbibed on top of two layers of filter paper (Whatman No.1) in 9 cm plastic Petri dishes. Sixteen treatments (four varieties × four light exposure durations) were applied to each temperature regime. Black plastic bags were used to seal the Petri dishes to reduce evaporation and to block the light. Germination test was conducted for 40 days and final germination percentage was recorded at the end of the test.

Comparisons were also made between germination counting under normal lab light and under green safe light. Fifty seeds were imbibed in each Petri dish as described in 3.2.2. Four temperature regimes, 15/25, 20/20, 5/15, and 10/10°C, were used. A RCBD with five replicates was used and replicates were put into growth chambers at weekly intervals. Eight treatments (four varieties × two types of light) were applied to each temperature regime. Germinated test was conducted 40 days and seeds were counted and removed under designed light source daily and the seeds with shoot greater than 3 mm were considered germinated.

The effects of applying fungicide (0.05% benomyl powder) to the seeds on seed germination were investigated under 15/25 and 5/15°C temperature regimes. A RCBD with five replicates was used and replicates were put into growth chambers at weekly intervals. Eight treatments (four varieties × two fungicide treatments) were applied to each temperature regime. The data collection method was the same as described in Part I.

Two methods to test seed variability, 0.1% Tetrazolium Chloride (TZ) solution (Grabe, 1970) and finger pressing, were also compared. Both methods were used on non-germinated seeds after the fungicide experiment was terminated. The viable non-germinated seeds and dead seeds were recorded.

8. Data analysis

In addition to modeling techniques described above, Analysis of Variance (ANOVA) was conducted using the GLM procedure for germination and viability data (SAS, 1995). Percentage data were transformed with arc sine square root prior to analyses. Treatment means were separated using Fisher's least significant difference (LSD) test at P = 0.05. Data were back-transformed for presentation.

The rate of seed germination was calculated using Germination Rate Index:

$$GRI=(G_{tot}/p)*(\sum g_i/t_i) \quad \text{(Eq. 13)}$$

where G_{tot} is the total number of germinated seeds at the end of the germination test terminated, p is the total number of seeds, and g_i is the number of seeds germinated between time t_{i-1} and t_i (h) (Holt and Orcutt, 1996; Steinmaus et al., 2000).

Part II: Seedling Emergence in the Field and its Prediction Using Thermal Time Model

1. Seed sources and site description

The same species and varites were used in this experiment. Seed cleaning and storage were done following the same procedures as described in Part I. Seeds were selected individually using tweezers to ensure that each seed was well formed, and then seeds were mixed with benomyl powder at a concentration of 0.05% (w/w) before seeding to prevent and reduce fungal infection.

Field trials were conducted at the field experimental station of Agriculture and Agri-Food Canada, Saskatoon Research Centre. The soil was a Dark Brown Chernozem (Typic boroll) clay at the experiment site (Matus-Cádiz and Hucl, 2003). The sand, clay and silt contents were 23, 45 and 33%, respectively. Field water capacity was 57%, and the soil bulk density was 1.14 g/cm^3 (top 5 cm of soil). Field plots were prepared to a similar soil surface condition using bedding harrows before seeding.

2. Periodicity of seedling emergence in the field

Four seeding dates were conducted in 2003 and 2004, respectively, which were 3 May 15 May, 27 May, and 8 June 2003, and 7 May, 19 May, 31 May, and 10 June 2004. A randomized complete block design (RCBD) with five replicates was used and the plot size was 1.0 m x 1.0 m. Sixteen treatments (four varieties × four seeding dates) were randomly allocated to each block each year. Within each plot, two hundred seeds were hand-sown evenly at 1 cm depth in four rows for easy seedling identification. Irrigation was provided once a day to the level of field capacity unless there was a significant precipitation event (> 5 mm) in the previous 24 hours and the soil was near its field capacity.

Soil temperatures at the sowing depth (1 cm) were recorded every minute using dataloggers (21X, Campbell Scientific Inc., USA). The average, maximum and minimum daily soil temperatures were used for thermal time model assessment. Seedling emergence in the field was monitored at 2-day intervals. Seedlings were counted as emerged when coleoptiles were visible from the soil surface and were removed after each counting. Seedling emergence rate index (ERI) was calculated using the same method as germination rate index (GRI) in Part I.

3. Comparison of seedling emergence with seed germination and the modification of the thermal time model

A growth chamber experiment was designed to establish the relationship between seed germination in Petri dishes and seedling emergence in soil. Two types of soil, field-collected soil

and Redi-earth® (artificial soil), were also compared. Field-collected soil was air dried, sieved and placed in seeding trays before water was added to the field capacity. Fifty seeds were spread on a level soil surface and covered with 1 cm of soil. The same seeding method was used for the Redi-earthPart I. Petri dishes and seeding trays were randomly placed in growth chambers (Conviron PGR15, Controlled Environment Limited, Canada). Seed germination in Petri dishes and seedling emergence from pots (10 cm × 10 cm × 8 cm) filled with soil were conducted in darkness at four temperature regimes including 15/25, 20/20, 5/15, and 10/10°C. Temperatures inside the chambers were recorded with dataloggers (21X, Campbell Scientific Inc., USA).

A RCBD with five replicates was used and replicates were put into growth chambers at weekly intervals. Twelve treatments (four varieties × three germination media) were applied to each temperature regime. Seeds with coleoptile greater than 3 mm in Petri dishes and seedlings visible at the soil surface were considered germinated or emerged, respectively. Seed germination and seedling emergence were recorded daily and the experiment was terminated after no new seedling emergence for 14 consecutive days. Seeds germinated or emerged were removed after each counting and water was added when necessary.

A supplemental experiment was conducted to further compare seedling emergence from field soil and Redi-earth® soil under field conditions. Four pots filled with Redi-earth® soil were buried in the field plots on the third seeding date in 27 May 2003. Fifty seeds were seeded in each pot to 1 cm deep. Seedling emergence from these containers was compared with that from the soil surface on the same seeding date.

4. Seed fate of previously buried seeds in the field

On each seeding date four steel mesh containers (10 cm x 10 cm x 4 cm) were placed in each plot. The bottom of the container was 3 cm below the soil surface and the container was covered with 2 cm of soil. Filter paper bags containing 50 seeds of each variety was placed horizontally in each container and covered with 1 cm of soil. These paper bags were retrieved after 2, 4, 6, and 8 weeks of burial. Seeds were removed from the paper bags after retrieval. Germinated seeds were recorded and then discarded. Non-germinated seeds were imbibed in Petri dishes at 15/25°C in darkness. Seed germination was counted at 24-hour intervals and seeds with coleoptiles greater than 3 mm were considered germinated. Germinated seeds were removed after counting and water was added when necessary. Viability of nongerminated seeds at the end of the germination test was tested using finger pressing method as describe in Part I.

5. Data analysis

Analysis of variance was conducted using GLM procedure of SAS program (SAS, 1995) for final seed germination/seedling emergence and ERI as affected by seeding dates, germination media and burial duration. The percent of seedling emergence data were transformed with arc sine square root. Treatment means were separated using Fisher's least significant difference (LSD) test at P = 0.05. The back-transformed means used to discuss the results of this experiment and they are shown in percentages.

The relationship pertaining the required thermal time for the corresponding subpopulations between the seed germination in the Petri dish and seedling emergence in soil in the growth chamber was established by Chapman-Richards function as:

$$y = \alpha(1 - \exp(-\beta x))^{\gamma} \qquad \text{(Eq. 14)}$$

where y = the relative thermal time for seed germination in the Petri dish, α = the asymptote, β =the rate parameter, and γ = the shape parameter, all of which were derived from the Chapman-

Richards function, x = the thermal time for seedling emergence in soil, which equals to $\sum_{i=1}^{t}(T_i - T_b)$ with the T_b was obtained in Part I.

A nonlinear regression procedure with the Levenberg-Marquardt algorithm method (Marquardt, 1963; SAS,1995) was used to estimate the germination/seedling emergence time for different subpopulations from seed germination time course in Petri dish and seedling emergence time course in the soil, and to estimate the parameters for the Chapman-Richards function. The final function of thermal time model for seedling emergence in the field was modified as:

$$\text{Seedling emergence (\%)} = a(1 - \exp(-by)^c \qquad \text{(Eq. 15)}$$

where a = the asymptote, b = the rate parameter, and c = the shape parameter, and y =the relative thermal time in the Petri dish in Eq. 14. All constants were from the thermal time models constructed in Part I using the 10°C temperature amplitude.

The modified thermal time models were used to predict seedling emergence in the field. The ability of the modified model to predict seedling emergence was determined by the coefficient of determination (R^2) of the linear regression analysis of the predicted against the observed seedling emergence. RMSE (root mean square error), SRES (sum of residuals) and SARES (sum of absolute residuals) between the predicted and observed seedling emergence were also calculated for each cultivar on each seeding date to estimate the variation and accuracy of thermal time models (Oryolot et al., 1997). A small RMSE would indicate that the predicted data were similar to the actual data (McMaster et al., 1992). The SRES and SARES would assess bias. If the SRES was smaller than the SARES, any errors tended to cancel one another. If both the SRES and SARES were large and the SARES was positive, the model would underestimate seedling emergence. If the SRES was negative and larger than the SARES, the model would overestimatE seedling emergence (McMaster et al., 1992).

Results

Part I: Effects of Temperature on Dormancy Change, Germination and the Application Of Thermal Time Model

1. Effects of temperature on germination and germination rate

Seed viability was 99.6% for 'Arctic' and 'Lineta', and 100% for 'Walsh' and 'LC9078a'. Seed germination of orchardgrass and western wheatgrass was affected by temperature and the optimal temperature for germination depended on variety. The final germination percentage of both species showed a bell shape response to temperature with an optimum temperature between 15-25°C (Figure 1). The final germination percentage of 'Arctic' and 'Lineta' was approximately 77% and 83% at optimal constant temperature, respectively. The final germination of the two Western wheatgrass, 'LC9078a' and 'Walsh', was less than 10% at constant temperatures.

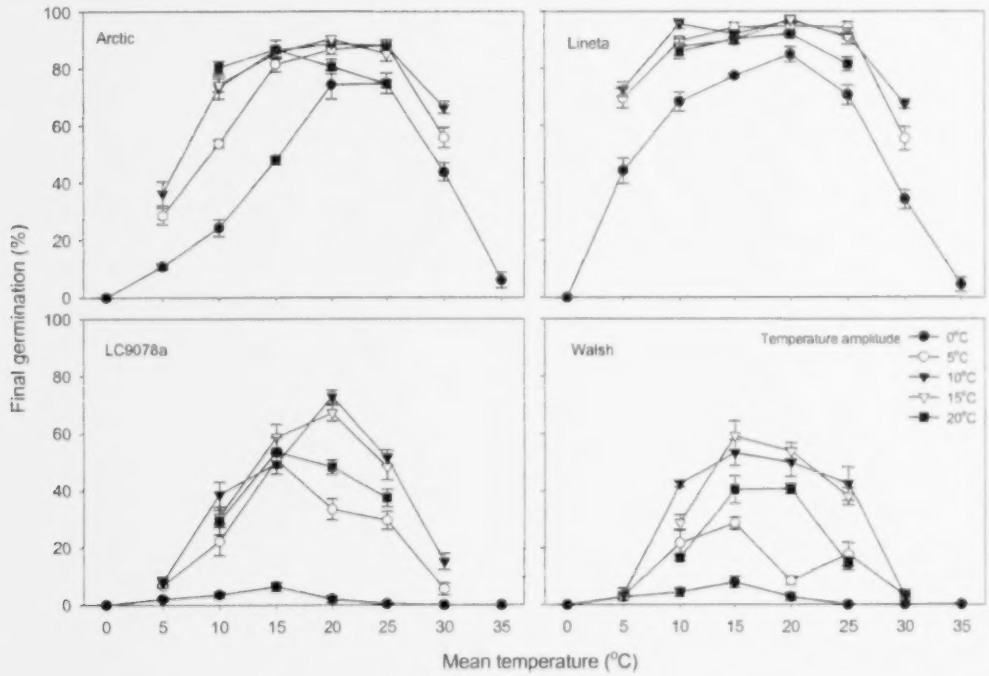

Figure 1. Final germination percentage of orchardgrass ('Lineta' and 'Arctic') and western wheatgrass ('LC9078a' and 'Walsh') under various temperature regimes. Data are means ± SE (n=5).

The final germination of both species was higher under alternating than constant temperature regimes with the same mean temperature (Figure 1), indicating that the alternating temperature can break seed dormancy of both species. Germination enhancement between 20 and 40% in 'Arctic' and between 20 and 30% in 'Lineta' by alternating temperature was observed. Dormancy breaking by alternating temperatures depended on their mean and amplitude as well as species and varieties. A 5 to 10°C temperature amplitude was sufficient to break dormancy in these varieties and further increase in the amplitude did not further increase germination (Figure 2).

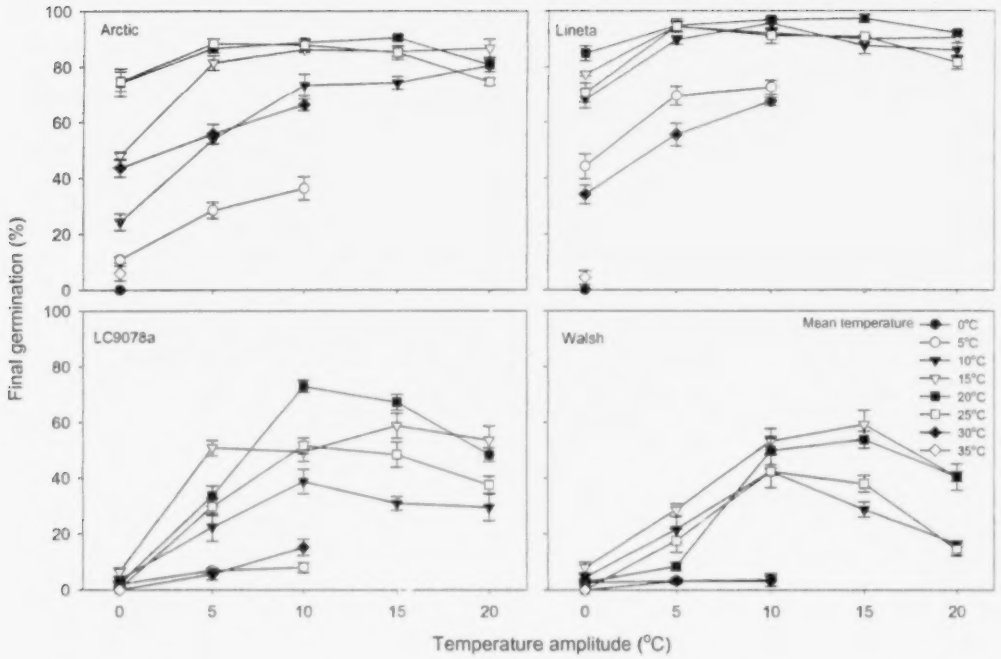

Figure 2. Effects of temperature amplitude on dormancy breaking of orchardgrass ('Lineta' and 'Arctic') and western wheatgrass ('LC9078a' and 'Walsh'). Data are means ± SE (n=5).

Germination rate as measured with GRI was generally higher under alternating temperature than constant temperature regimes with the same mean temperature (Figure 3). GRI was affected by alternating temperature similarly to that of final germination percentage.

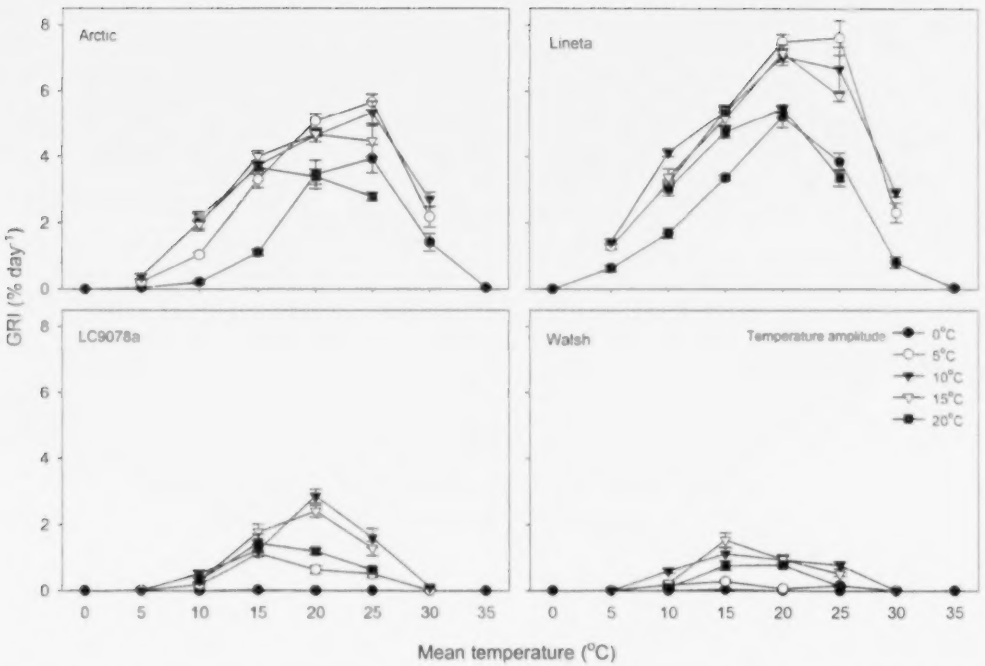

Figure 3. Germination Rate Index (GRI) of orchardgrass ('Lineta' and 'Arctic') and western wheatgrass ('LC9078a' and 'Walsh') under various temperature regimes. Data are means ± SE (n=5).

2. Modeling seed dormancy change as affected by temperature

The germination time course using Chapman-Richards nonlinear model had Pseudo-R^2 greater than 0.80 for most temperatures (data not shown). The sum of squares reduction test showed that there were common T_b's among subpopulations at 0, 5 and 10°C amplitudes for 'Arctic' and at 0, 5, 10, and 15°C amplitudes for 'Lineta'. Therefore, reduced models were used to estimate T_b for the two varieties at those temperature amplitudes (Figures 4, 5). The minimum requirement for regression could not be met for 'Arctic' with the 15°C amplitude (Figure 4). For both varieties, the temperature regime with 20°C amplitude did not have enough data points for the regression analysis and thus T_b could not be estimated (data not shown). The assumption of a common T_b among subpopulations could not be met for the two varieties of western wheatgrass, either due to the limited available subpopulations (low germination and high dormancy) or the parallel slopes of *GR* on *T* among subpopulations (Figures 6, 7).

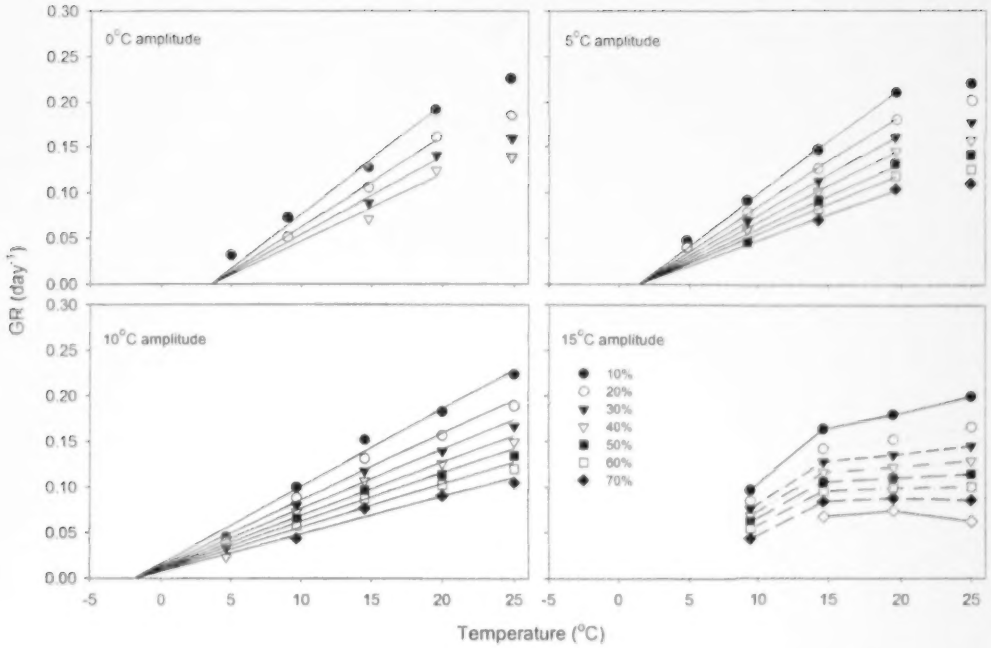

Figure 4. Germination rate (*GR*) of 'Arctic' orchardgrass within the range of sub-optimal temperatures as a function of temperature and sub-populations with various temperature amplitudes.

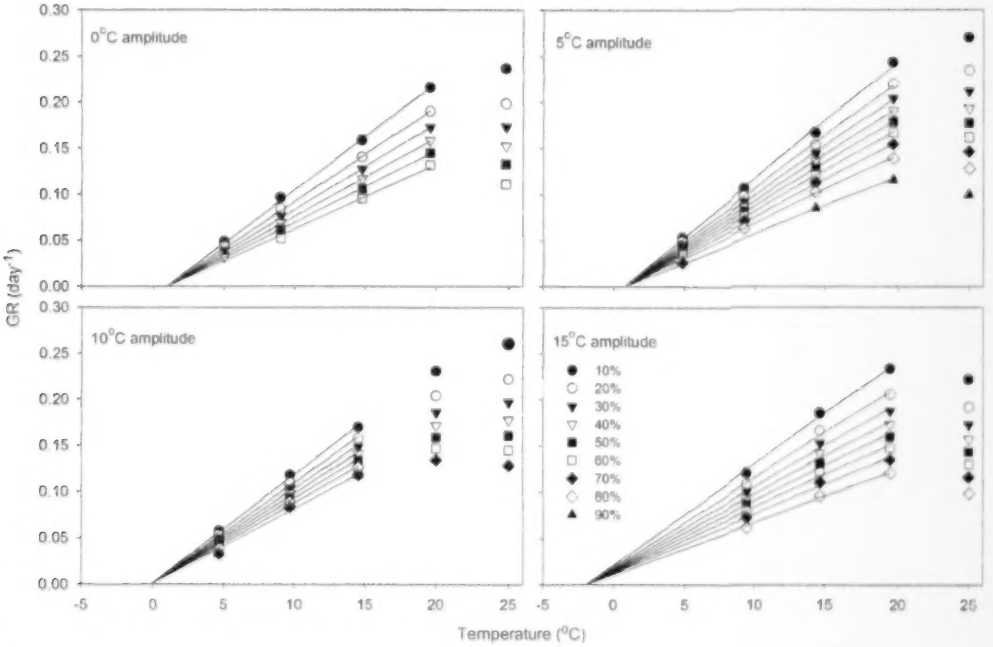

Figure 5. Germination rate (*GR*) of 'Lineta' orchardgrass within the range of sub-optimal temperatures as a function of temperature and sub-population with various temperature amplitudes.

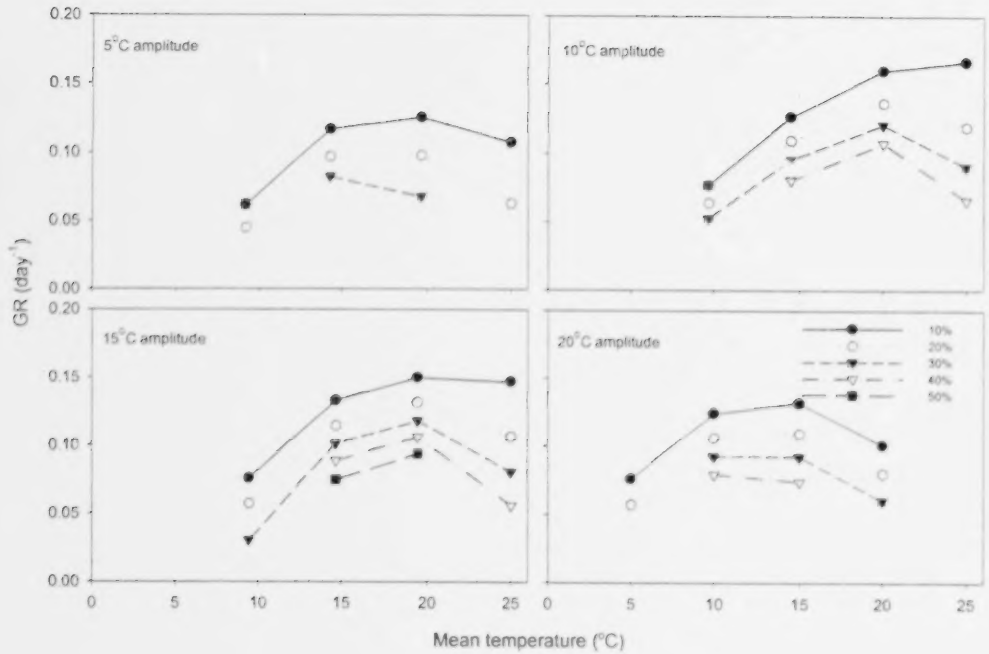

Figure 6. Germination rate (*GR*) of different subpopulations at different mean temperature for 'LC9078a' western wheatgrass under various temperature amplitudes.

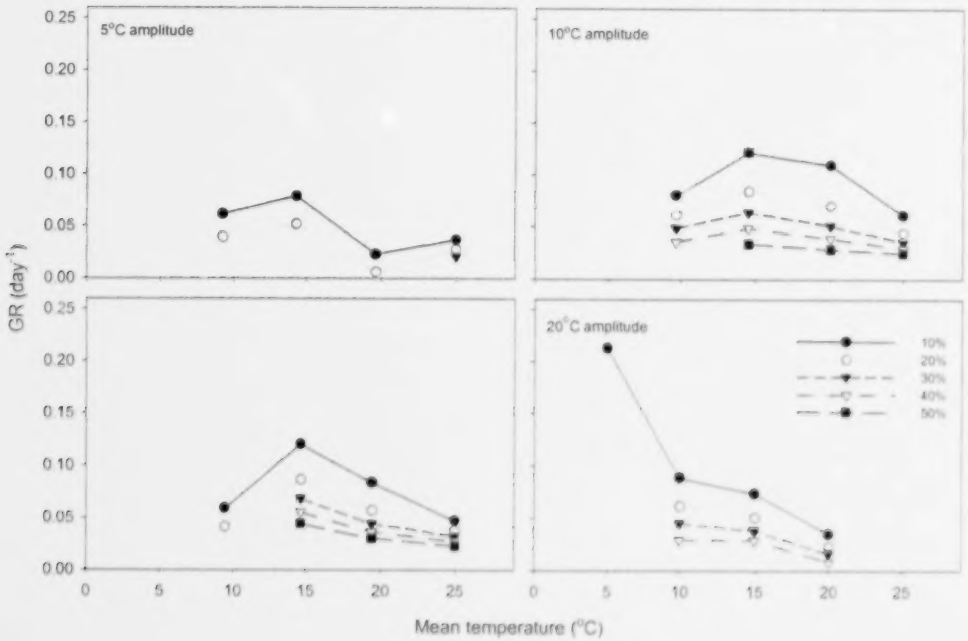

Figure 7. Germination rate (*GR*) of different subpopulations at different mean temperature for 'Walsh' western wheatgrass under various temperature amplitudes.

The T_b of 'Arctic' differed significantly among 0 (constant temperature), 5, and 10°C amplitudes, decreasing as the temperature amplitude increased (Table 2). The T_b of 'Lineta' also differed significantly among 0, 5, 10 and 15°C amplitudes, declined as the amplitude increased.

Table 2. The common base temperatures (T_b) among subpopulation and their 95% confident intervals (CI) for orchardgrass 'Arctic' and 'Lineta' at various temperature amplitudes estimated based on the reduced model.

Variety	Temperature amplitude (°C)	T_b (°C)	CI (°C)
'Arctic'	0	3.6	1.7 ~ 5.6
	5	1.4	0.8 ~ 2.1
	10	-1.9	-3.4 ~ -0.4
	15	NA	NA
	20	NA	NA
'Lineta'	0	0.93	0.7 ~ 1.2
	5	0.73	0.5 ~ 1.0
	10	-0.14	-0.6 ~ 0.3
	15	-1.93	-2.8 ~ -1.1
	20	NA	NA

Thermal time for different sub-populations based on the estimated T_b was affected by temperature amplitude (the inverse of the slopes of the lines in Figures 4 and 5). Thermal time models were constructed separately for each temperature amplitude using Champman-Richards growth function based on T_b's and thermal time (Table 3).

Table 3. Parameters describing the thermal time model (mean ± SE) derived from the Champman-Richards growth function for orchardgrass ('Arctic' and 'Lineta'). *a* = the asymptote; *b* = the rate parameter; *c* = the shape parameter.

Variety	Temperature amplitude (°C)	*a*	*b*	*c*
'Arctic'	0	67.4±7.0	0.024+0.003	12.8±3.0
	5	87.2±2.4	0.025±0.001	16.9±1.9
	10	84.7±0.9	0.019±0.000	18.9±1.0
'Lineta'	0	79.4±0.5	0.034±0.000	38.6±1.2
	5	93.9±0.3	0.047±0.004	91.5±3.5
	10	89.2±0.1	0.058±0.000	305.4±4.0
	15	91.6±0.1	0.033±0.000	42.8±0.4

The effects of alternating temperatures on germination rate could be reflected from the first and second derivatives of nonlinear thermal time model using the parameters value in Table 3 (Figure 8). The maximum germination (asymptote) of 'Arctic' was lower in 20/20°C (constant temperature) compared to 17.5/22.5 and 15/25°C (alternating temperatures). The highest daily germination (inflection point) was 13%, 15%, and 10% at 15/25, 17.5/22.5, and 20/20°C, respectively on the 8th, 7th, and 7th days. The rate of daily germination increased to the highest on the 5th, 4th, and 5th day at 15/25, 17.5/22.5, and 20/20°C, and then decreased to the lowest at the 10th, 8th, and 9th days, respectively.

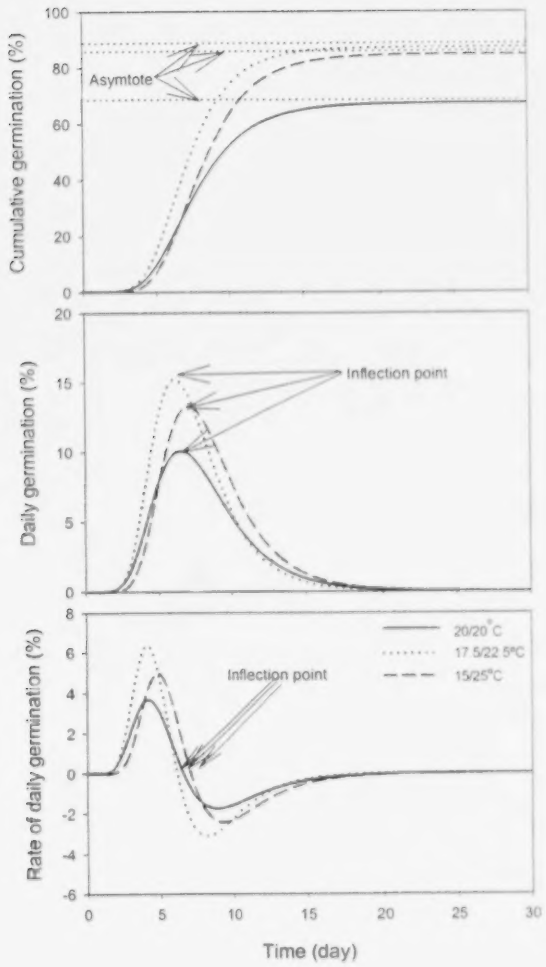

Figure 8. Cumulative germination percentage, daily germination percentage, and rate of daily germination of 'Arctic' orchardgrass expressed by thermal time model, first derivative of thermal time model, second derivative of thermal time models for 0, 5°C and 10°C amplitude temperature regimes with a mean temperature of 20°C.

The SRES was smaller compared to SARES (Figures 9, 10), thus errors tended to cancel on each other. Predicted germination time course fitted well with the observed data for both varieties at most temperatures as measured RMSE except for 'Arctic' at 0/10°C for which germination was overestimated by the model (Figure 9).

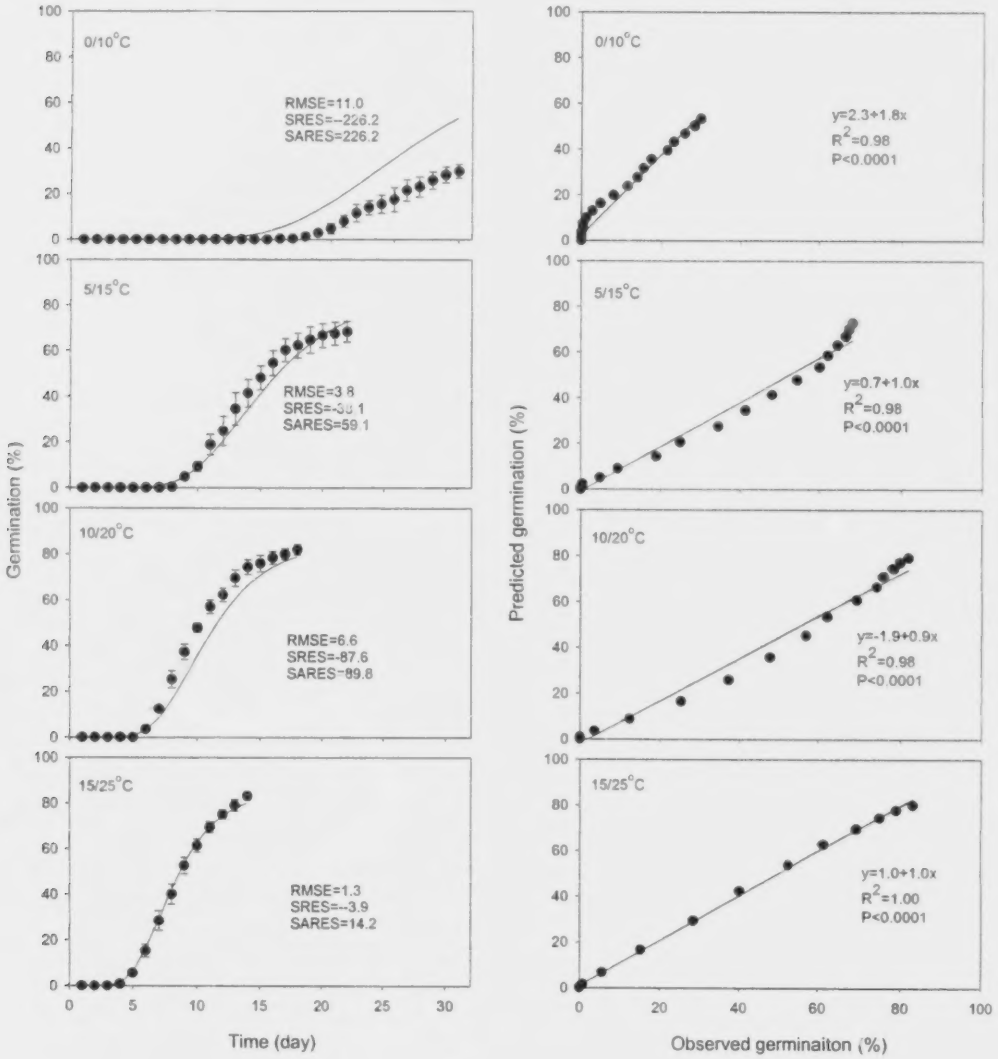

Figure 9. Simulated germination based on thermal time model (solid line) and observed germination (symbols) and model fit using regression analyzing for 'Arctic' orchardgrass with 10°C amplitude. Data are means ± SE (n=5).

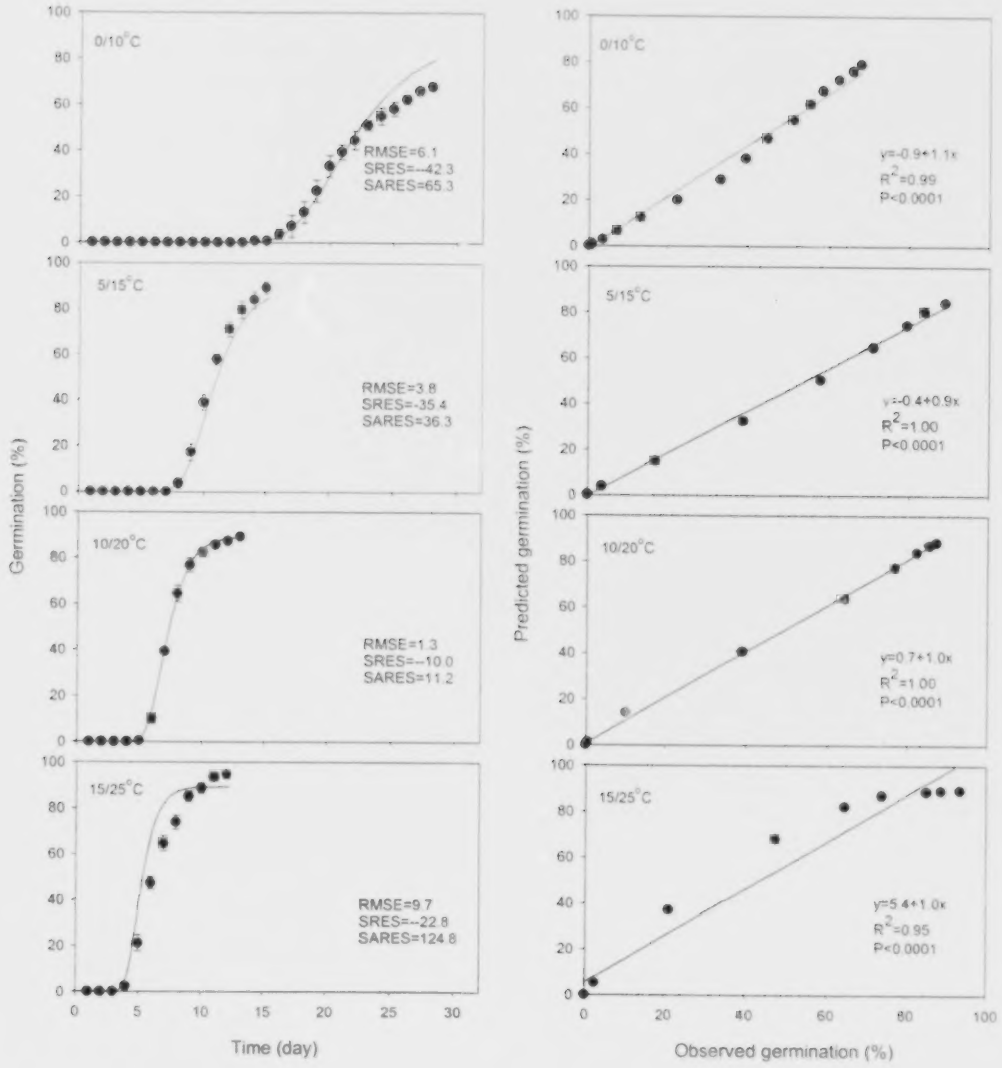

Figure 10. Predicted germination based on thermal time model (solid line) and observed germination (symbols) and model fit using regression analyzing for 'Lineta' orchardgrass with 10°C amplitude. Data are means ± SE (n=5).

3 Effects of light duration, light quality, fungicide and seed viability test method on germination

Exposure to light during germination check had minimal effect on the final germination percentage among 5, 10, and 15 minutes treatment of two varieties of orchadgrass and western wheatgrass at two alternating temperatures (Figure 11). Differences in final germination percentage among 5, 10, and 15 minutes light exposures were less than 5%, except for 'Walsh' that germination decreased with increasing duration of light exposure. Up to 25% enhancement in germination by light exposure was found in 'Arctic' at 5/15°C, and up to 14% reduction in germination was found in 'Walsh' at 15/25°C.

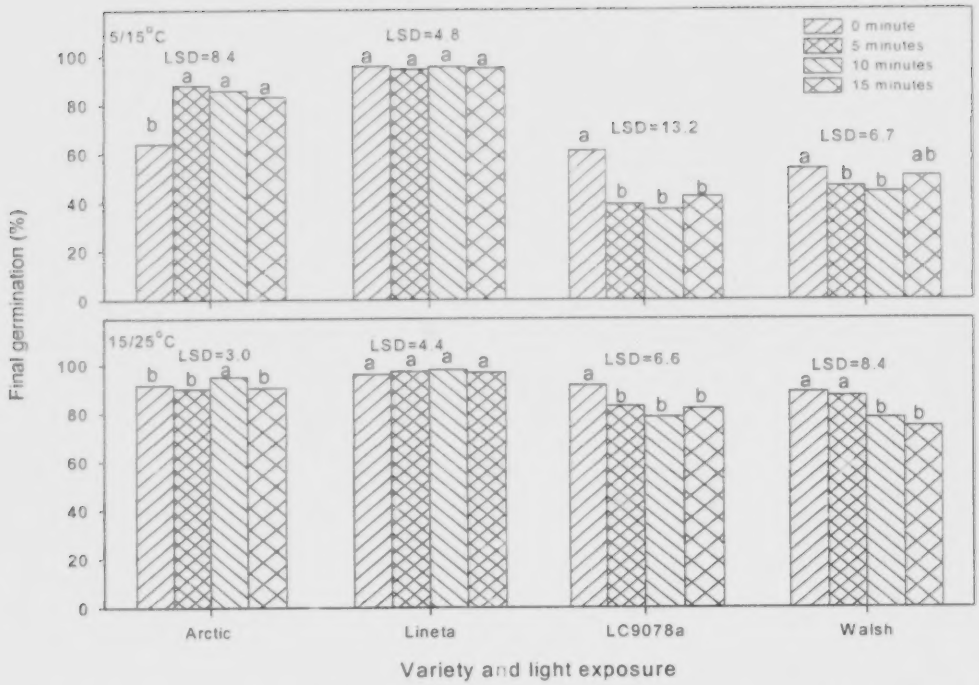

Figure 11. Final germination of orchardgrass ('Lineta' and 'Arctic') and western wheatgrass ('LC9078a' and 'Walsh') at 5/15 and 15/25°C as affected by the duration of light exposure. Means with the same letters were not significantly different at P≤0.05 within each temperature regime and each variety.

The effects of lab light and safe light during germination checking on seed germination were temperature specific for both species. Seed germination was higher under laboratory light than safe light for 'Arctic' at 20/20 and 15/25°C, but it was not significantly different at 10/10 and 5/15°C. Lab light stimulated seed germination for 'Lineta' at 20/20 and 5/15°C, but had no effects at 10/10 and 15/25°C. On the contrary, brief exposure to laboratory light during germination checking reduced germination of western wheatgrass at 10/10 and 5/15°C but not at 20/20 and 15/25°C (Figure 12).

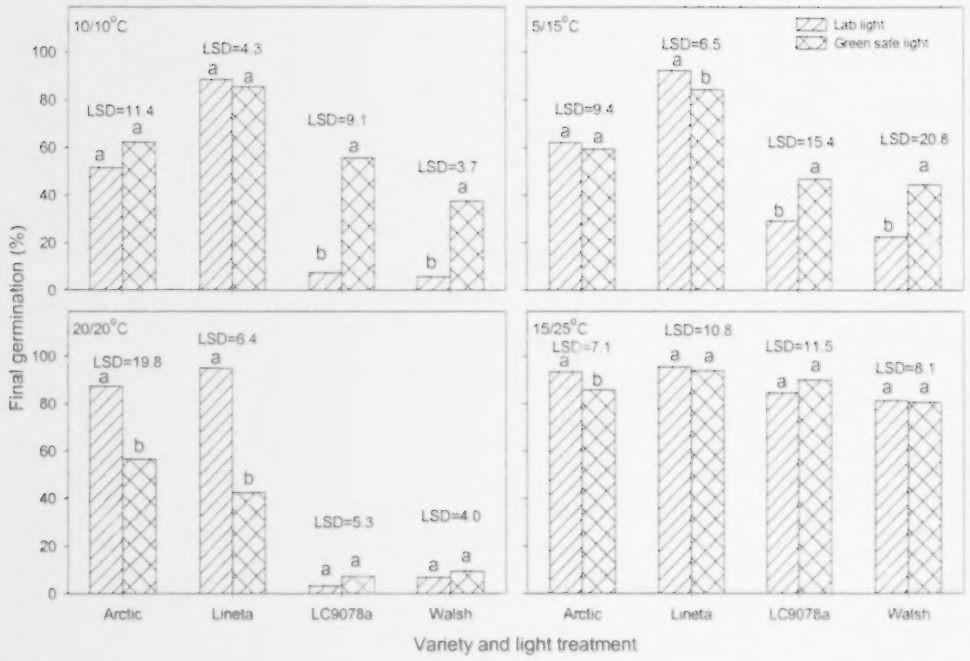

Figure 12. Final germination of orchardgrass ('Lineta' and 'Arctic') and western wheatgrass ('LC9078a' and 'Walsh') at 10/10, 5/15, 20/20, and15/25°C counted under normal lab light and green safe light. Means with the same letters were not significantly different at P≤0.05 within each variety and each temperature regime.

The application of fungicide (0.05% benomyl) had no significant effects on the final germination percentage for all varieties at 5/15 and 15/25°C except for 'Lineta' at 15/25°C which was 8.1% higher in fungicide treatment than the control. There were no significant effects for fungicide application on GRI for 'Arctic', 'LC9078a', and 'Walsh' at both temperature regimes except for 'Walsh' which had 0.1%day^{-1} decrease at 5/15°C. GRI of 'Lineta' increased 0.25 and 1.1%day^{-1} for fungicide application compared to the control at both temperature regimes (Figure 13).

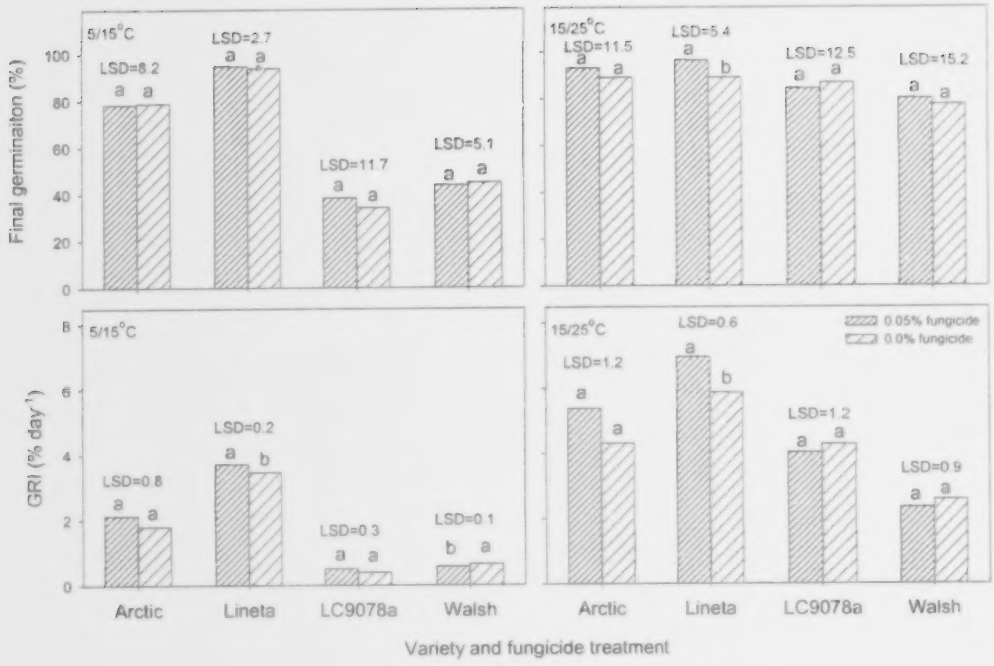

Figure 13. Final germination and Germination Rate Index (GRI) of orchardgrass ('Lineta' and 'Arctic') and western wheatgrass ('LC9078a' and 'Walsh') at 5/15 and 15/25°C temperature regimes with the application of 0.05% and 0% fungicide (benomyl powder). Means with the same letters were not significantly different at P≤0.05 within each temperature regime and each variety.

The paired t-test showed that there was no significant difference between finger pressing and the TZ method for seed viability in the two species (data not shown).

Part II: Seedling Emergence In The Field And Its Prediction Using Thermal Time Model

1. Seedling emergence in the field as affected by seeding date

The final percentage of seedling emergence in the field ranged from 47% to 92% in 2003 and from 47% to 91% in 2004 for the two species. Within orchardgrass species, there was no significant difference or decreased slightly on final percentage of seedling emergence between the two varieties, versus within western wheatgrass, 'Walsh' had an average of 28.5% and 46.4% higher seedling emergence than 'LC9078a' in 2003 and 2004, respectively (Figure 14). Seedling emergemce tended to decrease with seeding date in 'Arctic' and 'Lineta', two varieties of orchardgrass. In contrast, both 'LC9078a' and 'Walsh', two varieties of western whe. grass species, consistently had the significantly highest final percentage of seedling emergence from the third seeding date in both years, which was in late May (May 27 in 2003 and May 31 in 2004, respectively).

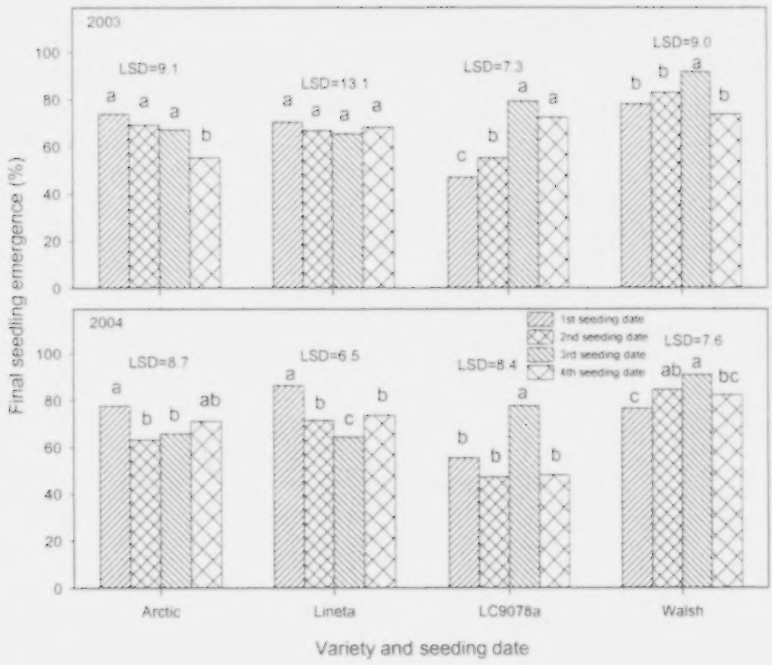

Figure 14. Final seedling emergence of two varieties of orchardgrass ('Arctic' and 'Lineta') and two varieties of western wheatgrass ('LC9078a' and 'Walsh') as affected by seeding date in 2003 and 2004. Means with the same letters within a variety were not significantly different at P≤0.05.

Seedling emergence rate index (ERI) of both orchardgrass varieties tended to be higher in the later seeding dates than in the earlier seeding dates in both 2003 and 2004 (Figure 15). Similar to the trend in final percentage of seedling emergence in western wheatgrass, ERI in this species tended to increase with seeding date, reaching the highest in the third seeding date.

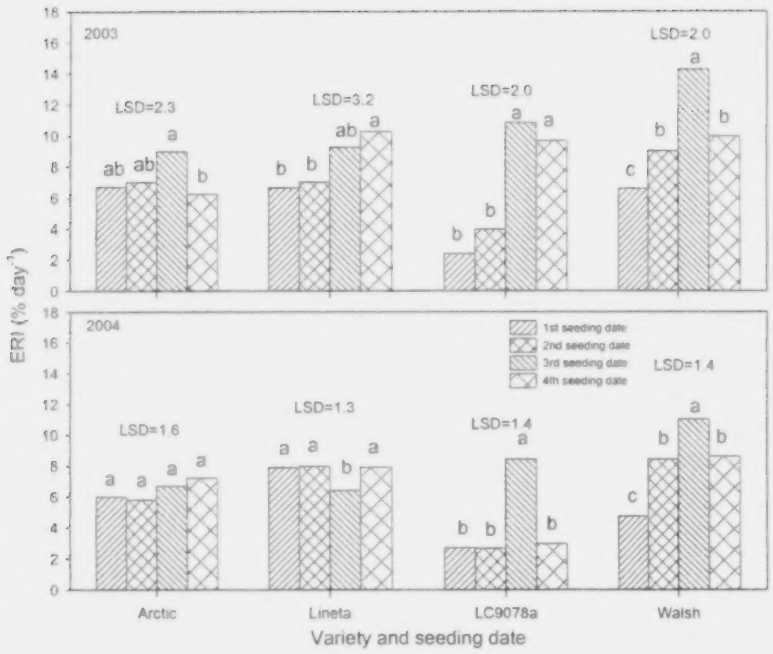

Figure 15. Seedling emergence rate index (ERI) of two varieties of orchardgrass ('Arctic' and 'Lineta') and two varieties of western wheatgrass ('LC9078a' and 'Walsh') as affected by seeding date in 2003 and 2004. Means with the same letters within a variety were not significantly different P≤0.05.

2. Comparison of seedling emergence in the soil with seed germination in Petri dishes

In growth chambers alternating temperature resulted in higher final seed germination/seedling emergence than constant temperatures for both species and higher temperature (20/20, 15/25°C) had higher final germination and seedling emergence than the corresponding lower temperatures (10/10, 5/15°C) (Figure 16). Seed germination was higher than seedling emergence from pots filled with field collected soil in orchardgrass at all temperatures. Seedling emergence from field soil was generally lower than that from Redi-earth® soil for orchardgrass at all temperature except for 20/20°C. Germination and seedling emergence were low at both constant temperatures for western wheatgrass. At both constant temperatures and the low alternating temperature (5/15°C), germination tended to be lower than seedling emergence from field soil. At 15/25°C, however, when germination and seedling emergence were highest, germination tended to be higher than seedling emergence. Seedling emergence tended to be higher in field soil than Redi-earth® soil for orchardgrass, which was true for western wheatgrass only at lower temperature (10/10, 5/15°C).

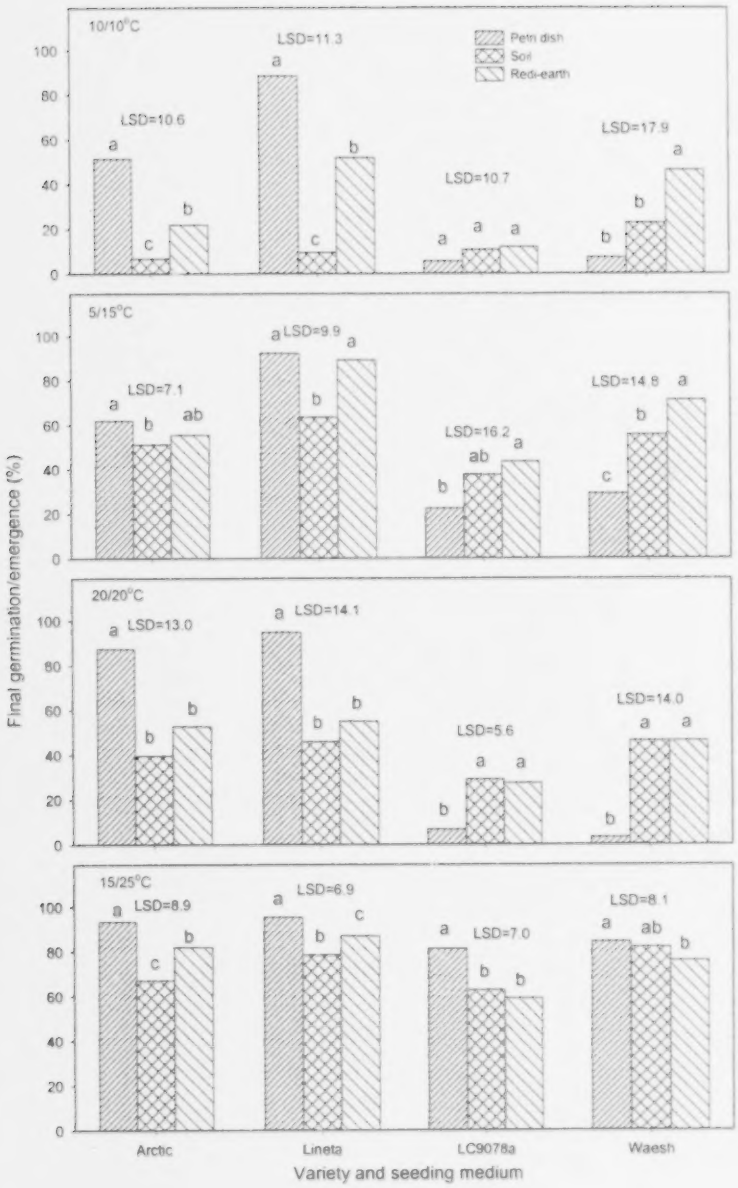

Figure 16. Effects of germination medium on germination/emergence of orchardgrass ('Arctic' and 'Lineta') and western wheatgrass ('LC9078a' and 'Walsh') at 10/10, 5/15, 20/20, and15/25°C. Means with the same letters within a temperature and variety were not significantly different at P≤0.05.

Under field conditions, the higher seedling emergence in Redi-earth® soil than field soil was found only in 'Arctic' but not in others (Figure 17).

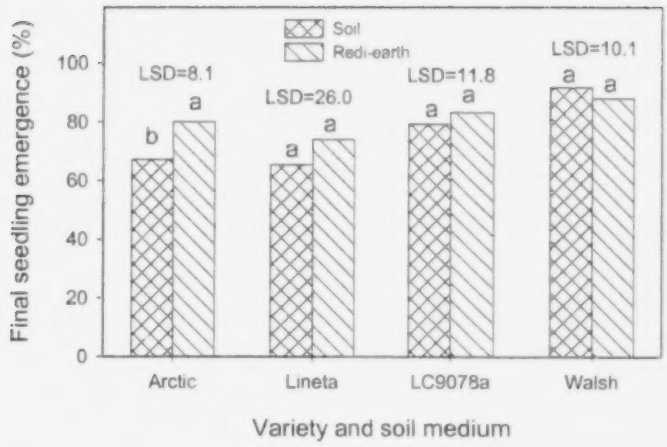

Figure 17. Final seedling emergence of orchardgrass ('Arctic' and 'Lineta') and western wheatgrass ('LC9078a' and 'Walsh') in the field as affected by soil medium type. Means with the same letters within a variety were not significantly different at $P \leq 0.05$.

3 Modification of the thermal time model for seedling emergence

The average temperature amplitudes at 1 cm depth of soil from each seeding date to the end of each seedling emergence period were 11.7, 10.8, 11.1, and 11.5°C in 2003 and 11.1, 9.4, 10.3, and 11.6°C in 2004 for the four seeding dates, respectively (Figure 18). The mean temperatures at 1 cm depth were 14.0, 15.7, 17.6 and 17.8°C in 2003 and 9.4, 12.7, 14.4 and 16.2°C in 2004 for the four seeding dates, respectively. Therefore, thermal time models with 10°C amplitude were used.

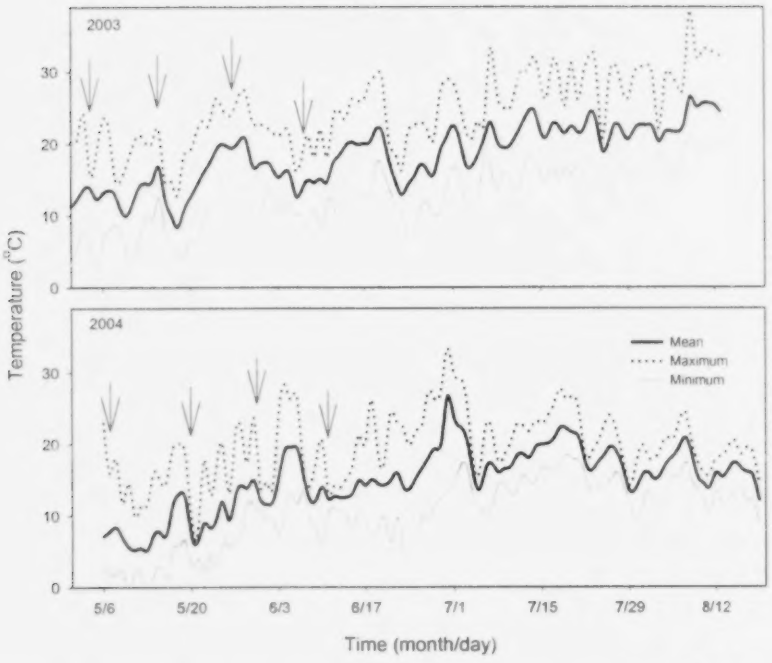

Figure 18. The daily mean, maximum, and minimum temperatures at 1 cm depth of soil during the growing season of 2003 and 2004. Arrows stand for seeding dates. (May 3, May 15, May 27, and June 8 in 2003 and May 7, May 19, May 31, and June 10 in 2004).

Thermal time models were not constructed for western wheatgrass due to its low germination and the lack of common T_b among subpopulation (Part I), thus, only orchardgrass was used to validate thermal time models in seedling emergence. The base temperature for each variety was adopted from thermal time models developed in Part I. The relationship of the thermal time between seed germination in the Petri dish and seedling emergence in the soil corresponding to the same subpopulation was established using Eq. 14 (Figure 19). Seedling emergence from the 1 cm depth in soil in the growth chamber required more thermal time accumulation than seed germination in Petri dishes for the same subpopulation in orchardgrass tested with the two varieties. The disparity of required thermal time between seedling emergence and seed germination was greater in 'Lineta' than in 'Arctic'. The required thermal time for seedling emergence and seed germination corresponding to the same subpopulations were well correlated by an exponential relationship for 'Arctic' ($R^2 = 0.62$) and 'Lineta' ($R^2 = 0.93$).

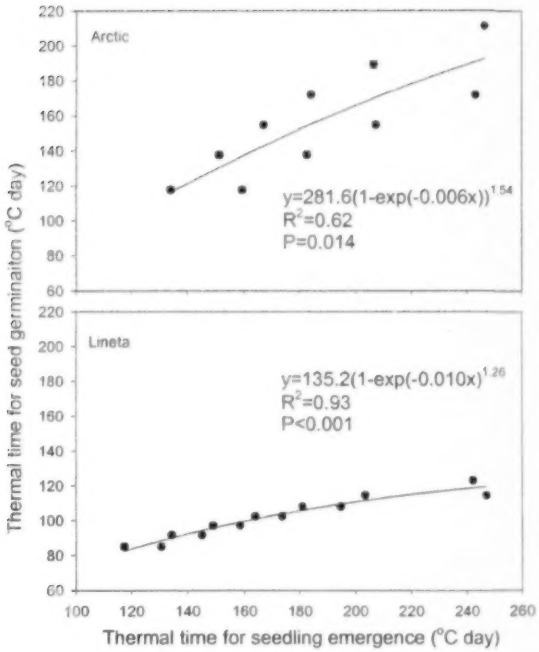

Figure 19. The relationship between the thermal time of seed germination corresponding to the same subpopulation of seedling emergence established using Chapman-Richards function at 15/25 and 5/15°C.

4. Predictability of modified thermal time models for seedling emergence in the field

The modified thermal time models successfully predicted seedling emergence in the field as indicated by the high R^2 (between 0.92 to 0.99) (Figures 20, 21, 22, 23). The RMSE was small (<15%), indicating that the predicated and measured seedling emergence was similar. However there was an overestimation for the 4th seeding date in 2003 (Figure 20) and underestimation for the 1st seeding date in 2004 (Figure 21) especially at the late stage of seedling emergence for 'Arctic'. Seedling emergence was underestimated in 'Lineta' for the first two seeding dates in 2004 (Figure 23).

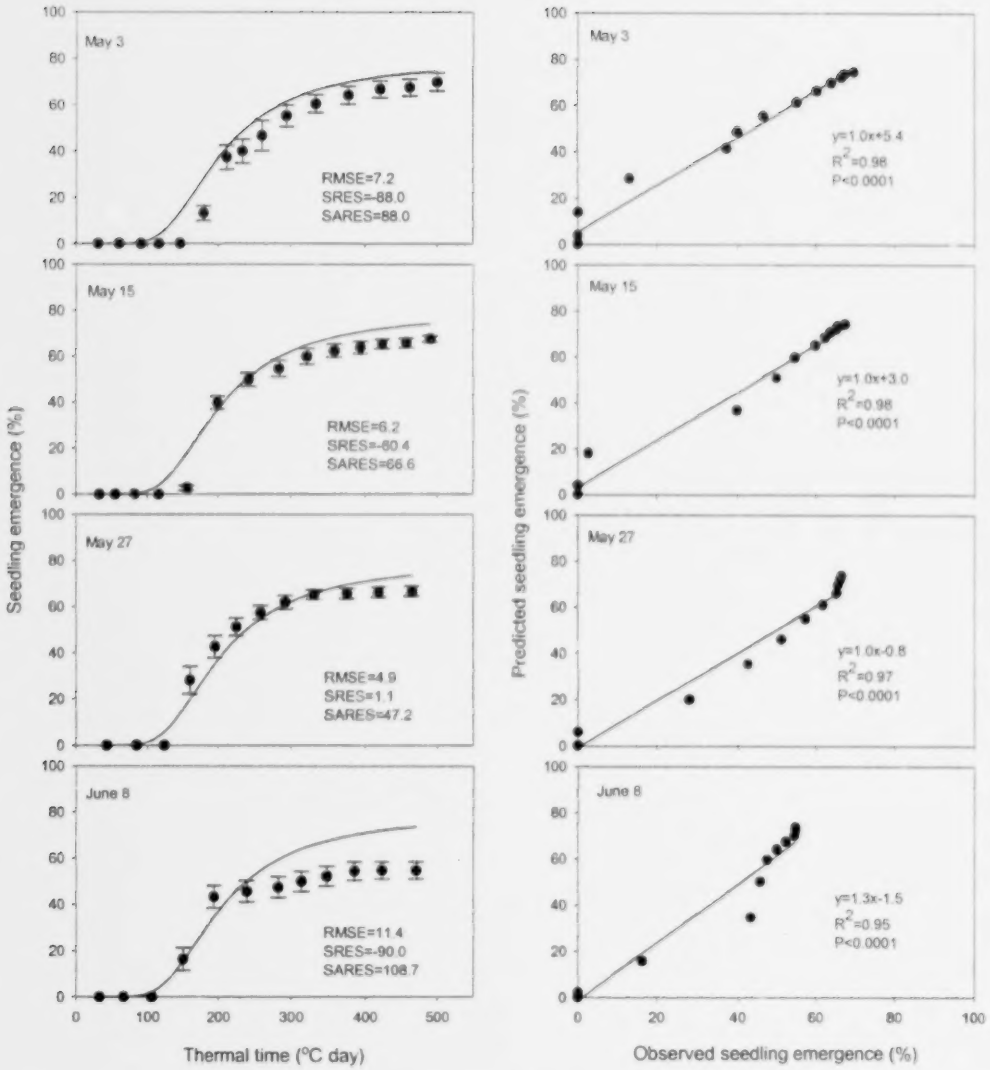

Figure 20. Predicted (solid line) and observed seedling emergence (symbols) for 'Arctic' orchardgrass in the field for four seeding dates in 2003. Data are means ± SE (n=5). Predicted seedling emergence was estimated using the modified thermal time model with 10°C amplitude.

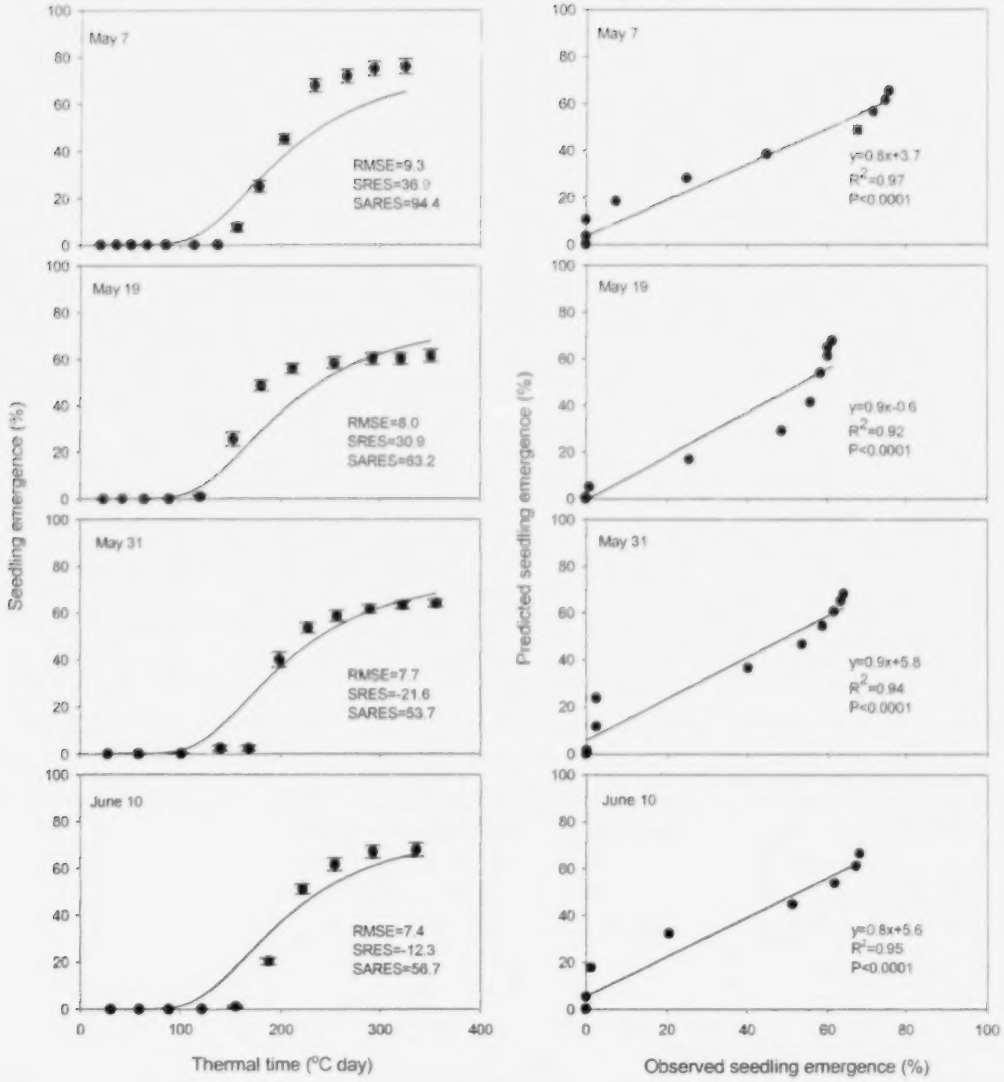

Figure 21. Predicted (solid line) and observed seedling emergence (symbols) for 'Arctic' orchardgrass in the field for four seeding dates in 2004. Data are means ± SE (n=5). Predicted seedling emergence was estimated using the modified thermal time model with 10°C amplitude.

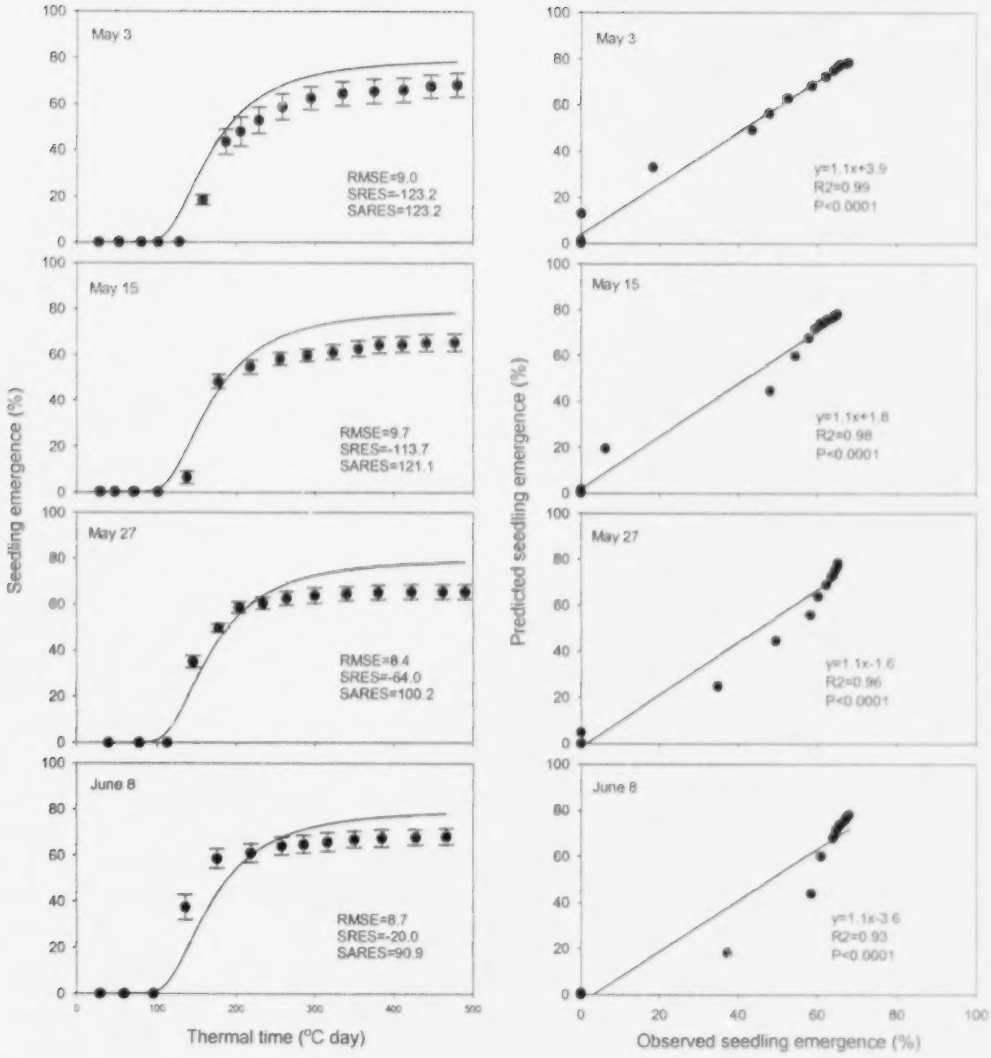

Figure 22. Predicted (solid line) and observed seedling emergence (symbols) for 'Lineta' orchardgrass in the field for four seeding dates in 2003. Data are means ± SE (n=5). Predicted seedling emergence was estimated using the modified thermal time model with 10°C amplitude.

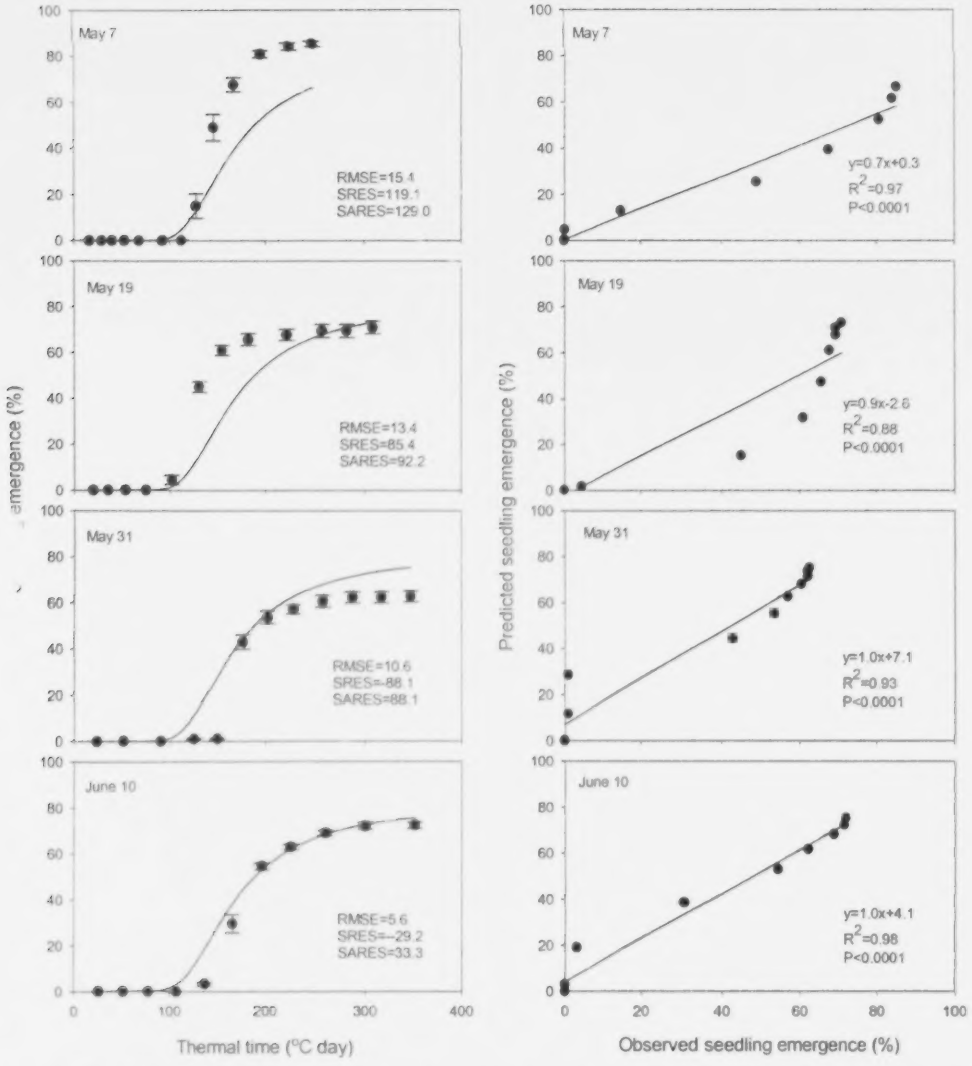

Figure 23. Predicted (solid line) and observed seedling emergence (symbols) for 'Lineta' orchardgrass in the field for four seeding dates in 2004. Data are means ± SE (n=5). Predicted seedling emergence was estimated using the modified thermal time model with 10°C amplitude.

5. Seed fate of previously buried seeds as affected by seeding date and burial duration

It is not surprising that the longer the burial durations the higher the germination occurred in the field with each seeding date both for orchardgrass and western wheatgrass (Tables 4, 5, 6, 7). However, seed mortality did not increase with increasing burial duration. The seedling emergence after 6 weeks burial was usually similar among seeding dates for orchardgrass and tended to increase with seeding dates for western wheatgrass. Percentage of dormant seeds was similar among seeding dates for orchardgrass but decreased with seeding dates for western wheatgrass. For 'LC9078a' the seed dormancy reached the lowest at third seeding date for both years. The dead seeds were similar among seeding dates in 2003, but were significantly increased after first seeding dates in 2004 for orchardgrass. However, the dead

seeds in the buried western wheatgrass were less than 10% and similar among seeding dates in both years.

Table 4. Effect of seeding date and burial duration on seed fate of 'Arctic' orchardgrass in 2003 and 2004. Germ: % seed germinated during burial, Non-dor: % germinated at15/25°C, Dor: % viable but not germinated in 15/25°C, and Dead: % decayed seeds.

	Burial	2003 seeding date					2004 seeding date				
Seed fate	duration (week)	1st	2nd	3rd	4th	$LSD_{0.05}$	1st	2nd	3rd	4th	$LSD_{0.05}$
Ger	2	53.0B†b‡	77.0Ba	75.3Ba	77.7Aa	**16.8**	36.1Bc	65.4ABab	75.4Ba	57.7Cb	**13.0**
	4	79.7Aa	79.5ABa	85.9Ba	81.3Aa	**11.3**	94.6Aa	65.2ABb	69.2Bb	59.3BCb	**12.7**
	6	79.3Aa	83.7Ba	82Ba	79.6Aa	**17.0**	82.8Aa	62.6Bb	75.9Bab	71.5Bb	**13.1**
	8	82.2Ab	87.3Aab	98.8Aa	87.6Aab	**12.1**	83.3Aa	76.8Aa	88.1Aa	89.1Aa	**14.7**
	$LSD_{0.05}$	**13.3**	**9.1**	**12.7**	**13.5**		**12.3**	**13.7**	**9.7**	**12.2**	
Non-dor	2	34.7Aa	5.6Ab	2.0Ab	1.1Ab	**10.7**	51.4Aa	12.1Ac	4.5Ad	27.2Ab	**7.6**
	4	9.5Ba	3.1ABb	0.5Ab	2.0Ab	**4.8**	0.0Cc	10.1Ab	6.5Ab	21.0ABa	**5.1**
	6	7.8Ba	0.5Bb	1.2Ab	3.2Ab	**3.4**	16.4Ba	6.1Ab	4.8Ab	13.2BCab	**8.5**
	8	3.8Ba	0.5Bb	0.0Ab	0.1Bb	**2.9**	7.2Ca	7.8Aa	2.1Aa	8.5Ca	**9.2**
	$LSD_{0.05}$	**12.3**	**3.8**	**2.5**	**2.7**		**7.7**	**8.3**	**5.5**	**8.5**	
Dor	2	9.4Ab	16.6Aab	22.3Aa	19.6Aa	**9.9**	6.8Aa	0.0Ab	0.0Ab	0.0Ab	**3.4**
	4	9.6Aa	15.8Aa	10.8Ba	14.7ABa	**9.8**	0.5Ba	0.4Aa	0.4Aa	0.0Aa	**1.1**
	6	11.6Aa	13.8Aa	5.3Ca	9.1Ba	**10.3**	0.4Ba	0.4Aa	0.4Aa	2.4Aa	**2.4**
	8	9.5Aa	7.0Aa	0.4Db	6.7Bab	**6.2**	0.4Bab	0.0Ab	0.8Aab	1.6Aa	**1.6**
	$LSD_{0.05}$	**5.2**	**10.2**	**3.4**	**10.2**		**3.7**	**0.7**	**1.2**	**2.5**	
Dead	2	2.9Ba	0.8Bab	0.4Ab	1.6Ba	**2.1**	5.6ABb	22.5Aa	20.1Aa	15.1Aab	**9.6**
	4	1.2Ca	1.6Ba	2.8ABa	1.9Ba	**3.0**	4.9ABb	24.3Aa	23.9Aa	19.7Aa	**11.7**
	6	1.3Cb	2.1ABab	5.3Bab	8.0Aa	**6.6**	0.4Bc	30.9Aa	18.9Ab	12.9Ab	**10.3**
	8	4.5Aa	5.2Aa	0.4Ba	5.6ABa	**5.8**	9.0Ab	17.4Aa	9.0Bb	0.8Bb	**8.4**
	$LSD_{0.05}$	**1.4**	**3.3**	**3.4**	**5.9**		**6.4**	**14**	**7.8**	**7.6**	

†Data followed by different upper-case letters within a column were significantly different at P = 0.05.

‡Data followed by different lower-case letters within a row were significantly different at P = 0.05.

Table 5. Effect of seeding date and burial duration on seed fate of 'Lineta' orchardgrass in 2003 and 2004. Germ: % seed germinated during burial, Non-dor: % germinated at15/25°C, Dor: % viable but not germinated in 15/25°C, and Dead: % decayed seeds.

Seed fate	Burial duration (week)	2003 seeding date					2004 seeding date				
		1st	2nd	3rd	4th	$LSD_{0.05}$	1st	2nd	3rd	4th	$LSD_{0.05}$
Ger	2	63.2B†b‡	75.6Bab	81.4Bab	85.9Ba	**18.6**	74.9Ba	70.0Aa	72.2Ba	74.7Aa	**13.9**
	4	84.0Aa	85.3Aa	77.2Ba	84.3Ba	**8.8**	95.8Aa	73.7Ab	76.5Bb	82.7Ab	**12.0**
	6	80.9ABbc	90.6Aab	73.3Bc	98.8Aa	**13.6**	90.4Aa	83.4Aa	85.3Aa	83.2Aa	**8.7**
	8	80.1ABc	91.7Aab	97.1Aabc	87.4B	**9.6**	88.3Aa	73.7Aab	79.8ABab	81.0Ab	**9.9**
	$LSD_{0.05}$	**20.2**	**8.8**	**9.8**	**8.6**		**9.3**	**15.0**	**8.0**	**9.2**	
Non-dor	2	19.8Aa	8.3Aab	1.6Ab	1.2Ab	**16.4**	20.2Aa	4.8Bb	4.4Ab	13.9Aa	**8.9**
	4	3.7Ba	2.1Aab	0.0Bb	0.8Ab	**2.3**	0.4Bb	14.0Aa	3.8Ab	7.4Bab	**6.9**
	6	1.6Ba	0.4Aa	0.8ABa	0.0Aa	**1.6**	5.1Ba	5.7Ba	0.0Bb	5.2Ba	**4.0**
	8	3.3Ba	1.0Ab	0.0Bb	0.0Ab	**2.2**	2.9Bab	7.1ABa	0.3Bb	5.4Ba	**4.7**
	$LSD_{0.05}$	**14.6**	**8.4**	**1.1**	**1.3**		**8.0**	**8.1**	**2.4**	**5.6**	
Dor	2	13.1Aa	15.7Aa	15.8Aa	12.1Aa	**11.1**	2.4Aa	0.8Ab	0.0Ab	0.0Bb	**1.1**
	4	11.1Ab	12.1ABb	22.0Aa	11.5Ab	**7.7**	0.9Ba	0.0Bb	0.0Ab	0.0Bb	**0.8**
	6	15.2Aa	7.3Bab	16.4Aa	0.8Bb	**12.0**	0.4Ba	0.0Ba	1.2Aa	1.2Aa	**2.3**
	8	11.1Aa	5.8Bab	1.9Bb	6.7ABab	**6.9**	0.4Bb	0.0Bb	0.8Ab	4.3ABa	**3.1**
	$LSD_{0.05}$	**10.2**	**7.6**	**9.2**	**6.6**		**1.3**	**0.8**	**1.6**	**9.2**	
Dead	2	3.9ABa	0.4Ab	1.2Bb	0.8Bb	**2.7**	2.5Bb	24.4Aa	23.4Aa	11.4Ab	**9.3**
	4	1.2Bab	0.4Ab	0.8Bab	3.3ABa	**2.7**	2.9Bc	8.5Bbc	16.7ABa	11.3Aab	**7.8**
	6	2.3ABb	1.8Ab	9.4Aaa	0.4Bb	**3.0**	4.1Bb	10.9Bab	13.5Ba	10.4Aab	**6.9**
	8	5.4Aab	1.5Abc	1.0Bc	5.9Aa	**4.1**	8.5Ab	19.2ABa	19.1ABa	9.4Ab	**8.3**
	$LSD_{0.05}$	**3.9**	**2.6**	**3.3**	**2.9**		**4.2**	**10.8**	**9.5**	**6.5**	

†Data followed by different upper-case letters within a column were significantly different at P = 0.05.

‡Data followed by different lower-case letters within a row were significantly different at P = 0.05.

Table 6. Effect of seeding date and burial duration on seed fate of 'LC9078a' western wheatgrass in 2003 and 2004.Germ: % seed germinated during burial, Non-dor: % germinated at15/25°C, Dor: % viable but not germinated in 15/25°C, and Dead: % decayed seeds.

Seed fate	Burial duration (week)	2003 seeding date					2004 seeding date				
		1st	2nd	3rd	4th	$LSD_{0.05}$	1st	2nd	3rd	4th	$LSD_{0.05}$
Ger	2	22.0B[†]c[‡]	39.5Bb	72.0Ba	63.7Ba	**10.5**	15.2Bc	31.4Bb	65.1Aa	33.6Bb	**11.3**
	4	33.0Bb	39.5Bb	71.6Ba	71.1Ba	**13.2**	51.5Ab	53.3Ab	78.0Aa	40.7ABb	**14.6**
	6	45.4Ac	58.5Ab	86.4Aa	64.0Bb	**10.5**	51.7Ab	52.6Ab	76.8Aa	47.0Ab	**7.3**
	8	47.4Ab	52.2Ab	85.9Aa	83.7Aa	**13.1**	47.0Ac	56.9Ab	80.1Aa	44.2Ac	**7.9**
	$LSD_{0.05}$	**11.4**	**9.6**	**6.7**	**10.5**		**9.6**	**7.6**	**17.4**	**9.7**	
Non-dor	2	25.3Aa	13.2Ab	4.2Ac	6.2Ac	**6.6**	48.5Aa	23.3Ab	15.2Ab	17.6Ab	**12.5**
	4	12.0Ba	9.6ABab	1.9ABbc	1.2Cc	**8.2**	0.9Bb	4.4Ca	5.7Ba	6.3Ba	**3.5**
	6	7.6Ba	3.7Bb	0.0Bb	3.8Bb	**4.7**	5.5Ba	2.1Cb	5.3Bab	3.2Bab	**3.4**
	8	5.6Ba	3.6Bab	3.8Aab	0.4Cb	**3.9**	2.1Bb	7.4Ba	1.2Bb	7.3Ba	**3.7**
	$LSD_{0.05}$	**10.0**	**6.4**	**3.6**	**1.9**		**8.2**	**2.9**	**5.7**	**6.4**	
Dor	2	51.1Aa	45.3ABa	17.4Ab	26.4Ab	**10.3**	33.5Ba	42.4Aa	18.1Ab	40.8Ba	**11.0**
	4	52.6Aa	49.2Aa	19.9Ab	23.5Ab	**13.9**	45.1ABa	42.2Aa	14.2Ab	51.8Aa	**13.8**
	6	40.1Aa	37.0Ba	10.1Bc	22.9Ab	**10.6**	42.8ABa	43.2Aa	15.1Ab	50.0ABa	**9.8**
	8	46.2Aa	43.8ABa	7.5Bb	12.6Bb	**14.0**	48.4Aa	34.0Ab	14.2Ac	47.7ABa	**9.9**
	$LSD_{0.05}$	**12.9**	**11.0**	**5.7**	**7.0**		**12.5**	**10.7**	**12.6**	**10.5**	
Dead	2	1.5Ab	2.0Ab	6.4ABa	3.7Bab	**3.4**	2.8Ab	2.8Ab	1.6Ab	8.0Aa	**4.0**
	4	2.4Ab	1.7Ab	6.7Aa	4.1Bab	**3.2**	2.6Aa	0.0Ab	2.0Aa	1.3Bab	**2.0**
	6	1.5Ab	0.8Ab	3.5BCb	9.3Aa	**3.9**	0.0Ba	2.1Aa	2.8Aa	0.0Ba	**3.2**
	8	0.8Aab	0.4Ab	2.8Cab	3.2Ba	**2.8**	2.5Aab	1.6Ab	4.4Aa	0.8Bb	**2.3**
	$LSD_{0.05}$	**3.1**	**2.2**	**3.1**	**3.8**		**1.9**	**3.8**	**3.0**	**3.0**	

[†]Data followed by different upper-case letters within a column were significantly different at P = 0.05.

[‡]Data followed by different lower-case letters within a row were significantly different at P = 0.05.

Table 7. Effect of seeding date and burial duration on seed fate of 'Walsh' western wheatgrass in 2003 and 2004. Germ: % seed germinated during burial, Non-dor: % germinated at15/25°C, Dor: % viable but not germinated in 15/25°C, and Dead: % decayed seeds.

	Burial duration	2003 seeding date					2004 seeding date				
Seed fate	(week)	1st	2nd	3rd	4th	$LSD_{0.05}$	1st	2nd	3rd	4th	$LSD_{0.05}$
Ger	2	42.4B†c‡	61.2Bb	85.9Ca	80.6Ca	**16.4**	21.6Cb	70.4Ba	78.0Ba	70.8Ba	**9.0**
	4	70.9Ab	76.8ABb	87.4Ca	89.6ABa	**10.6**	78.7Aa	73.9ABa	84.9ABa	76.4ABa	**12.9**
	6	73.8Ac	83.5Ab	94.0Ba	95.0Aa	**5.6**	65.6Bc	79.5ABb	89.2Aa	79.2ABb	**8.9**
	8	80.0Ab	86.0Ab	97.9Aa	85.9BCb	**8.7**	88.9Aab	79.1Ac	92.5Aa	83.1Abc	**9.0**
	$LSD_{0.05}$	**11.0**	**17.0**	**3.6**	**7.1**		**12.0**	**8.9**	**9.5**	**11.9**	
Non-dor	2	36.7Ab	26.3Ab	5.9Aa	10.7Aa	**15.6**	65.7Aa	17.2Ab	13.9Ab	16.8Ab	**10.1**
	4	14.3Ba	9.1Bab	4.0ABbc	0.8Bc	**5.7**	0.0Cb	8.3Ba	9.0ABa	11.0Aa	**7.9**
	6	10.4Ba	6.5Bb	0.4Bc	1.1Bc	**3.7**	14.0Ba	5.4Bb	2.0Cb	8.7Aab	**7.8**
	8	6.4Ba	4.8Ba	0.5Bb	0.8Bb	**3.7**	5.3Cab	9.3Ba	3.4BCb	4.8Aab	**5.3**
	$LSD_{0.05}$	**8.7**	**13.0**	**3.6**	**2.5**		**8.6**	**7.2**	**6.9**	**12.5**	
Dor	2	19.3Aa	11.0Ab	6.6Ab	7.5Ab	**4.4**	9.9Ba	10.4ABa	6.9Aa	9.6Aa	**6.5**
	4	13.4ABa	13.3Aa	7.9Aa	9.2Aa	**8.7**	18.4Aa	15.8Aab	4.0Bc	10.2Ab	**6.1**
	6	12.2ABa	8.8Ab	4.0Bc	1.9Bc	**3.2**	20.0Aa	13.5Aab	5.2ABc	8.9Abc	**7.5**
	8	11.2Ba	8.3Aa	1.0Cb	8.2Aa	**5.5**	4.9Ba	4.4Ba	3.3Ba	6.0Aa	**5.4**
	$LSD_{0.05}$	**7.9**	**7.4**	**2.3**	**3.8**		**7.8**	**6.2**	**2.6**	**7.0**	
Dead	2	1.6Aa	1.6Aa	1.5Aa	1.2Ba	**1.0**	2.8Aa	2.0Ba	1.2Aa	2.8Aa	**3.6**
	4	1.6Aa	0.8Aa	0.8ABa	0.4Ba	**2.2**	2.9Aa	2.0Ba	2.0Aa	2.4Aa	**2.8**
	6	3.6Aa	1.2Aa	1.6Aa	1.9Ba	**2.5**	0.4Ba	1.6Ba	3.6Aa	3.2Aa	**3.5**
	8	2.4Ab	0.9Ab	0.5Bb	5.1Aa	**2.6**	0.8ABc	7.2Aa	1.7Abc	5.7A	**4.4**
	$LSD_{0.05}$	**3.1**	**1.9**	**0.9**	**2.4**		**2.1**	**3.9**	**4.0**	**4.2**	

†Data followed by different upper-case letters within a column were significantly different at P = 0.05.

‡Data followed by different lower-case letters within a row were significantly different at P = 0.05.

Discussion and Management Implications

Seedling emergence of orchardgrass and western wheatgrass was affected differently by seeding dates in the field. In this project, only spring seeding was studied. The final seedling emergence of orchardgrass was either similar among the four seeding dates or it decreased slightly (<18%) as seeding date was delayed from early May to early June. The rate of seedling emergence either increased with later seeding dates or it was not different among seeding dates for orchardgrass. For western wheatgrass, however, final seedling emergence and the rate of seedling emergence increased with seeding dates from early to late May and decreased in early June. Once released from dormancy, seeds respond to temperature by changing their germination rate (Benech-Arnold et al., 1990a, b) and seeds germinate faster in warmer temperatures than in cooler temperatures (Garcia-Huidobro et al., 1982a). The increased rate of seedling emergence with seeding date has also been reported in many other species (Benech-Arnold et al., 1990a, b; Benech-Arnold et al., 2000; Meyer et al., 2000; Batlla et al., 2003). Seedlings emerged from late spring seeding dates in the Northern Great Plains, however, may have to face the adverse environmental conditions such as drought.

The two orchardgrass varieties tested had less seed dormancy than the two western wheatgrass varieties with the former having a broader range of temperature for dormancy breaking and germination (10-25°C) than the latter (peaked at 15°C). Seeds with less seed dormancy can germinate over a wider range of temperatures than seeds with deeper dormancy (Batlla et al., 2003). Final seedling emergence is usually similar within the optimum temperature range for non-dormant seeds (Garcia-Huidobro et al., 1982a) or seeds with low dormancy (Forcella et al., 2000). Soil temperatures at the seeding depth generally increased from the early May to late May and then decreased after the fourth seeding date. Therefore, the response of seeds to temperature explained the effect of seeding date on seedling emergence of both species.

Germinationof the previously buried seeds indicates that orchardgrass and western wheatgrass have the potential for a high germination percentage under field conditions for all seeding dates. Usually less than 10% of western wheatgrass seeds died after burial.Orchardgrass, however, had higher seed mortality than western wheatgrass especially when soil temperatures were increasing. Therefore, while soil temperatures close to the optimal temperature for dormancy breaking and germination promote germination of orchardgrass, the same conditions also cause deterioration of seeds if they fail to germinate. That seedling emergence increased with seeding dates for western wheatgrass is attributed to more loss of seed dormancy with the increasing temperatures among seeding dates.

The final germination percentage for orchardgrass was greater in Petri dishes than seedling emergence from soil media under controlled conditions. Under the same set of conditions, germination of western wheatgrass was less in Petri dishes than seedling emergence from soil. These can be partly explained by their response to light during seed germination. This study as well as previous reports indicate that light exposure enhances germination in orchardgrass (Probert et al., 1985), but exposure to light inhibits germination in western wheatgrass (Schultz and Kinch, 1976; Toole, 1976). The 1 cm seeding depth in the soil media should have eliminated or reduced exposure of seeds to light while seeds in Petri dishes were exposed to light when germination was checked. For small seeded species such as orchardgrass, mechanical impedance of soil can reduce seedling emergence (Bretagnolle et al., 1995). Greater seedling emergence from Redi-earth® than from clay soil confirmed that orchardgrass is sensitive to mechanical impedance of soil. Under field conditions, other factors, such as soil

microbial and invertebrate activities, may interact with temperature and moisture, affecting seedling emergence (Garvin et al., 2004; Wang, 2005).

Different oxygen conditions in germination media may also cause disparities between seed germination and seedling emergence. In this study, the coleoptile of orchardgrass and western wheatgrass protruded earlier than the radicle in Petri dishes. Radicle emergence of western wheatgrass was much slower than that of orchardgrass. Earlier protrusion of the coleoptile than radicle in grass seeds may be due to oxygen deficiency as noted by Wijte and Gallagher(1996), and it may serve as a mechanism for avoiding growing into oxygen-depleted media (Forcella et al., 2000). The slow radicle growth in western wheatgrass implies that western wheatgrass is more sensitive to oxygen deficiency than orcahrdgrass and proper germination media should be used for this grass.

The modified thermal time model accurately predicted (R^2=0.92 to 0.99) seedling emergence of 'Arctic' and 'Lineta' in the field in both years. This accuracy may be due to the use of alternating temperature regimes for the construction of thermal time models and the modification of thermal time models for seedling emergence. Predictive threshold models developed in laboratory are usually based on seed germination at constant temperatures (Fyfield and Gregory, 1989; Finch-Savage and Phelps, 1993; Finch-Savage et al., 1998; Hardegree and Van Vactor, 1999). It is not surprising that most of these models cannot accurately predict germination patterns in the field (Fyfield and Gregory, 1989; Finch-Savage et al., 1998; Hardegree and Van Vactor 1999) because of fluctuating temperatures in the field. Fluctuating temperatures can modify parameters in the thermal time model such as T_b for seeds with some degree of dormancy. For western wheatgrass, however, thermal time models could not be constructed because the linear relationship between germination rate and temperature cannot be established due to deep seed dormancy. An alternative way to construct the thermal time model for western wheatgrass is to first break seed dormancy using alternating temperature treatment, then establish the relationship between germination rate and constant temperatures. Further studies on the effects of alternating temperatures on dormancy release and modifications on thermal time model are needed for predicting seedling emergence in the field for species such a western wheatgrass.

Total seedling emergence and the rate of seedling emergence are important for stand establishment. This research quantified the effect of field conditions on dormancy changes and seedling emergence of orchardgrass and western wheatgrass in the field. Furthermore, quantifying the effects of field conditions on germination can be used to determine seeding rates for different seeding dates and to predict seedling densities under various temperature conditions. Different responses of orchardgrass and western wheatgrass to seedbed temperatures should be considered in determining seeding dates to maximize stand establishment. The thermal time model shows great promise for developing seeding rates for forages, and ultimately improving the success of stand establishment. However, parameters for thermal time models must be developed for each species and variety of forage.

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